



# QUANTITATIVE ECOLOGY

*A New Unified Approach*

Clarence Lehman | Shelby Loberg | Adam Clark

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## Quantitative Ecology: A New Unified Approach

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ISBN: 978-1-946135-53-7

Edition: 1.0

University of Minnesota Libraries Publishing  
Minneapolis, Minnesota



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PUBLISHING

## Cover Story

The day begins and ends on earth in beauty—a softly pigmented pageant for nature’s twice-daily changing of the guard. A powerful hailstorm chilled the air, prompting the lake to generate its own fog as the sun set beneath clouds dissipating in the west. There are only a few thousand exquisite sunsets in a human lifetime. Keep some of them for yourself and let them into your heart.

—C.ℒ., *Bloms Lake, Labor Day 2014*

## Preface

When I started teaching ecology on my own a few years ago, it became clear how the equations of ecology could be reformulated and unified to be more complete and easier to teach. The reformulation unfolded in steps, a little each year, with the students in the class contributing discussion and ideas. During the first two years we used a standard textbook, but that was not ideal because it did not match the form of the equations we were developing in class. In the third year we used no textbook, but that was not ideal either. So we now are supplying this textbook in an ebook format. It will not be ideal either, because it will still be evolving, but is part of a process that will advance with time.

The source material was prepared by Clarence Lehman, Shelby Loberg, and Adam Clark, initially using lecture Material from the fall 2015 class of Ecology 3407 at the University of Minnesota. Lectures were recorded each day and later transcribed by Larissa Little, work funded by a grant to Shelby Loberg from the University of Minnesota Libraries and led by Shane Nackerud. Copy-editing for the book was conducted by Susan Everson<sup>★</sup>.

Text recorded during lectures has a spoken style that can be rather different from written style, with repetition and review based on interaction with an audience. Larissa played the transcriptions of our lectures into earphones and



re-dictated the material into voice recognition software on her laptop computer, creating text files that were edited further by Shelby. I then them edited them further still, and put them into a printable form that included material from lecture slides. Adam Clark will work on exercises and other elements to be included in subsequent versions. These will be available here★.

It is not clear that this recording–transcribing–editing approach is the best way to create a textbook, but thus far it seems far superior to writing it from scratch. We first intended to use one of the emerging formats for ebooks, such as Pressbook, but they did not have sufficient power for representing mathematics, and did not yet have automatic numbering for figures and so forth. Accordingly, I wrote a little software package for creating technical ebooks called HTM-tex, which is an ebook-like syntax in front of Donald Knuth’s typesetting system  $\text{\TeX}$ ★—a system designed for producing beautiful books, especially those with mathematics. This should allow us to adapt to future ebook software as it develops.

We offer this to students with hopes that it will be as useful to them as their interactions have been to us.

—C.ℒ., August 2017

## Ebook versus book

An ebook is a book, but with special features. The version you are reading is sized to be read on your phone, tablet, or computer. Its pages are therefore smaller than those of a full-size textbook and its type is perhaps slightly larger, but still within the range of normal books if you print it.

One of the features is an active table of contents, appearing ahead. If you click on a page number in the contents, you will jump forward to that page in the book. The back-navigation arrow on your viewing software will then bring you back where you were. (You may have to enable the navigation arrows in your viewing software if they aren't automatically enabled. Alternatively, Alt-Left or Command-Left or Right may work.) From anywhere in the book, if you click on the small blue star in the upper right of the page, you will jump to the table of contents.

When you click on a word or phrase in blue, like the color of **this** word, you will jump to some other place. This blue text could indicate the number of a page containing something relevant, or the number of a figure on the same page or a different page; it could also be a web link. At the lower left in some figures is a white circle with a blue star. If you click on it, you will see an enlarged figure, or an animated version, or a set of related figures, or some further information about the figure.

In addition, a small blue star to the right of a phrase provides further information on a topic, often in Wikipedia.★ We expect some criticism for using Wikipedia, since it is often thought of as changeable and unreliable. However, since you can readily access the exact version of every article as it appeared at any time in the past, it is not really changeable, and our experience is that it is reasonably reliable for most scientific topics. Moreover, if you find unclarities or inaccuracies, you can readily fix them. It is thus becoming the most complete repository of evolving knowledge ever developed, and we want to take advantage of it.

Ebooks can be highlighted, annotated, and searched for phrases within them, depending on features of your viewing software. Passages can be copied for inclusion in notes or quotations, and can also be selected and read aloud by your computer. You may find that listening while reading, or listening by itself, helps understanding. Or you may not; with an ebook, it's your decision. (You may have to enable the reading-aloud feature in your viewing software if it is not automatically enabled.)

In an ebook you can also move instantly from one page to the next to view figures with successive parts and to see the development of each part. We have tried to arrange such figures at the tops of successive pages, or on full pages, as in the four pages beginning with Figure 16.13. (You should enable single-key forward and backward paging in your viewing software if it is not automatically enabled.)

An advantage to us is that an ebook is easy to change—so we can keep this one as clear and accurate as possible. Each

new version, no matter how small its difference from the prior version, is marked with a version identification number and a date, as you can see in fine print below for the version you are reading now.

We have tried to write this in a light, informal, second-person voice, rather than in the pedantic and formal tone some textbooks assume believe there is enough inevitable formality in the mathematics and computer code already, and we wish to make up for that.

On the use of the word “we,” as in the paragraphs above, we find this a difficult word to use consistently. Typically, when we say we, we mean the three co-authors of this book, though sometimes we mean, collectively, all of humanity. The meaning should be clear from context, we hope.

In any case, please tell us about any places where we could make this book more clear, accurate, or complete. We are eager to have this be a useful textbook offering.

—*C.L., S.L., A.C.*



A final advantage of an ebook is that there are no page-publication costs, so we can include discretionary pictures. Above, for your enjoyment, are two loons rendered by John James Audubon, ★ 1887–1969, one of the world’s great wildlife artists.

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## Chapter 1

### What is ecology?

Winston Churchill<sup>★</sup> pointed out that “All the great things are simple, and many can be expressed in a single word—freedom, justice, honor, duty, mercy, hope.” Should we try to define these? Can we define them?

We should at least try to define our subject, ecology; many textbooks start with definitions. But first, for background, consider how we might define life. Marvin Minsky<sup>★</sup> was an artificial intelligence researcher and computer scientist who thought about definitions. When is an object alive? Think about viruses, genes, self-reproducing machines—no one has really been able to give a good definition of “living” that satisfies in general. Some things are clearly living—mice—and some clearly are not—rocks. Lists of what makes something living used to appear in textbooks:

- (1) Self-reproducing
- (2) Responds to stimuli
- (3) Metabolizes
- (4) Made of protoplasm—protein, carbohydrates, DNA.

But (1) puts out the mule, (2) and (3) put out the spore, while if those conditions are dropped, (4) will admit the frankfurter. One can go on to extend the list with more careful qualifications, but questions remain until the list grows to include special mention of everything we can think of.

## 1.1 Definitions of ecology

With caveats in mind, consider definitions of ecology. In the 1860s, Ernst Haeckel,★ combined the term *oikos*—a place to live, home, habitat—with *logia*—discourse, study—to coin the word “ecology.” In the 1890s Ellen Richards★ included humans and harmony, quite a modern view. Variations over the years are shown in Table 1.1.

Haeckel	1860s	The total relations of an organism to its organic and inorganic environment
Richards	1890s	Living in harmony with the environment, first including family, then community, then the world and its resources
Elton	1920s	Scientific natural history
Odum	1960s	The study of the structure and function of nature, including the human species
Andrewartha	1960s	The scientific study of the distribution and abundance of organisms
Krebs		The scientific study of the interactions that determine the distribution and abundance of organisms
Molles	1990s	The study of relationships between organisms and the environment
Eilts	2010s	Life in context
Pope Francis	2015	The relationship between living organisms and the environment in which they develop

**Table 1.1.** *Various views of ecology.*

Each of these definitions has merit, but the first two and the last two are closest to the way the term is applied in this book. We humans have become prominent in ecology, locally to globally. No modern treatment of ecology is complete without a strong dose of anthropology.

The definition by Andrewartha has been widely quoted, but focusing merely on distribution and abundance reduces ecology to mapping, which is why Krebs modified this definition. The Pope's definition from his 2015 Encyclical includes the interesting idea of development, which can be taken to mean short-term development like embryogenesis and growth, plus long-term development like evolution. Overall, the definition by Eilts is perhaps the most general and engaging.

First and foremost, the most important concepts in ecology are about relationships, plus all of life, the whole environment, the processes of living and development, and, above all context. And in today's world, harmony. But also consider, "Poetry is the subject of the poem" (Wallace Stevens, 1937) and perhaps "Ecology is what ecologists do." With these in mind, we strive in the remainder of this book to define a theoretical form of ecology through examples and demonstrations, representative models and symbols, patterns and explanations, and lessons and caveats.



**Figure 1.1.** *The Rhind Papyrus, c. 1640 BC. One of the oldest known documents—and containing exercises from theoretical ecology!*

## 1.2 Ecology then and now

Our early hominin ancestors needed aspects of ecology. To find blueberries or other fruit, or where to dig wild onions, they had to know where these foods grew—their distribution and abundance. These parts of ecology have thus been part of life for hundreds of thousands of years. Ecology is connected with our species.

Some elements of the field of ecology were formalized more than 3000 years ago. The Rhind Papyrus (Figure 1.1) lists a number of ecological exercises for students—mathematics from ancient Egypt. Among these oldest ecological problems is this:

*Number 27. If a mouse eat 521 ikats of grain each year and a cat kills 96 mice a year, in each of 24 barns, how many cats are required to control the destruction of stored grain?*

This is a little problem in quantitative ecology! Even 36 centuries ago, mathematical ecology was part of life. Knowing how many grain bins determined how many cats were to be employed.

Today, ecology has become a glamour word. A product called “Ecogate,” for example, is part of a central vacuum system that keeps sawdust and sanding dust from being tracked around. But why the word Ecogate? Dust collection *per se* has nothing to do with ecology. Advertisers, however, have found that consumers respond positively to the term.

The term “ecosystem” is frequently used in business and finance, but there it means a collection of companies, customers, and products and their interconnections. For better

or worse, ecological terminology is expanding to other domains.

### 1.3 Methods of ecology

How do ecologists do ecology? Often, they start with observation, then move to theory—trying to fit observations together to make sense as a whole. Theory then leads to expectations, which in turn lead to experiments. Commonly, experiments aren’t undertaken until there is some theory to be tested and understood.

- (1) Observation
- (2) Theory
- (3) Experiment
- (4) Serendipity

Observation, theory, and experiment, however, are not the whole story. A large part of science turns out to be serendipity—luck and chance—capitalizing on chance and doing something with it. One example is Alexander Fleming★, who discovered penicillin. Some of the bacterial cultures in his lab became contaminated with penicillium mold and the cultures died. That ruined his experiment.

He could have written a memo to the laboratory staff ordering “Always keep mold away from our bacterial cultures. It destroys the cultures and will ruin the hypotheses we are trying to test.” But instead he capitalized on the serendipity, wondered what was happening, and found a substance in penicillium mold that kills bacteria. Fungi and bacteria have been archenemies for perhaps a billion years. Fleming’s



discovery has helped physicians actually *cure* disease, rather than being limited to diagnosing and prognosticating.

Following up on chance is, then, a large part of science. By the way, for an interesting paper, read the original 1929 report by Fleming about penicillium. It is so understated. He writes “the name ‘penicillin’ has been given to filtrates of broth cultures of the mould.” No one had heard of the word before. Then he suggests that “it may be an efficient antiseptic.” One of the greatest discoveries of all time and only, “it may be an efficient antiseptic.”

Cedar Creek★ is a University of Minnesota research site about thirty miles north of the University’s Saint Paul campus, and is one of the classic ecological research sites in the world. Pictured in Figure 1.2 is an experiment set up by Prof. David Tilman★. While very carefully designed, it came about because of serendipity—the chance event of a deep two-year drought that altered the abundances of species in a particular way and triggered the idea for this experiment.

Keep your eyes open for such chance events; they can crop up anywhere.



**Figure 1.2.** Observations and experiments testing theory at Cedar Creek★. This entire experiment was established following up on serendipity.

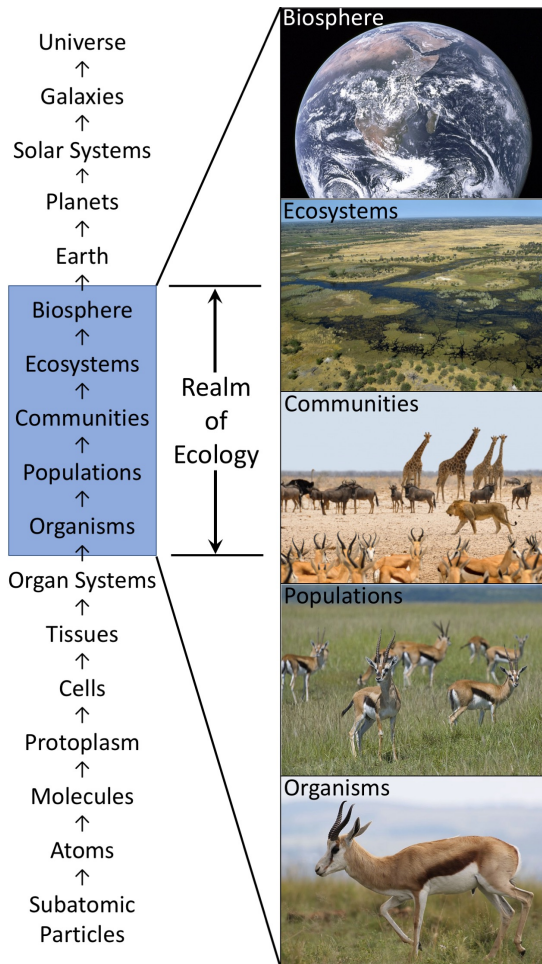
## Chapter 2

### Ecological theory

#### 2.1 Levels of ecology

Ecology covers a vast range of topics and can be viewed on multiple levels. One level is that of the *individual organism*—a single bacterium, an individual wolf pup. This includes individual behavior and physiology, with behavior as part of ecology. *Population ecology* covers groups of organisms of the same species—a bison herd or a grove of maples. *Community ecology* looks at how different populations interact, and the communities examined can be quite large. Above this level is *ecosystem ecology*, which examines how different communities interact with their environments. Finally, there is global ecology—ecology of the planetary ecosystem.

Individual ecology	Single organisms, behavior, and physiology
Population ecology	Groups of organisms from a single species
Community ecology	Populations of interacting species
Ecosystem ecology	Multiple communities and the environment
Global ecology	The planet as a biosphere

**Figure 2.1.** *Levels of complexity.*

## 2.2 Role of theory

From its early days, ecology has been in part a theoretical–mathematical science, and it is now also a computational science. Mathematical theory arises where systems are relatively simple. In our modern era, computation can address somewhat more complex systems, though creating computations on complex systems that satisfy the basic tenets of science is still problematic. For very complex systems, narrative is all we have available.

Examine the levels in Figure 2.1 to think about where theory applies. Subatomic particles and atoms are the realm of quantum mechanics, one of the most sublime and successful theories. Theory applies nicely to the hydrogen atom, a two-particle object. And while it applies to larger atoms, the raw mathematics becomes too complex as the number of particles grows, so computation comes into play. At higher levels like the molecular one, theory is harder to apply. Organic chemistry, for example, is not a strongly mathematical science, and at the level of protoplasm and cells there is no comprehensive mathematical theory or computational equivalent. This level is far too complex—with minuscule molecular machines running along tubules and carrying mitochondria on their backs at high speed relative to their size, it is more complex than any industrial factory. At the level of tissues and organs systems, we have only narratives to guide our understanding.

What happens, then, at the level of organisms, at the entry to ecology? Individual organisms are exceedingly complex. There is no complete mathematical theory for the

internal operation of individual organisms. But externally, organisms behave as a unit and populations become simpler than individuals—glossing over heartbeat, neuron firing rates, white blood cell replication, and so on, with all their enormous complexity. Details disappear. Populations can be described with basic mathematics. Communities are more complex, but are still within the reach of mathematics and, particularly, within the reach of computation. And ecosystems are complex, but with some unifying properties.

The whole earth thus begins to be simpler, and at the level of planets and solar systems, things once again become nicely mathematical. This is the level where, with Newton, modern science was born. In part, this emerging simplicity is because levels of detail again merge together. At the level of planetary orbits, it does not matter that dinosaurs once dominated the planet or that Mozart ever wrote any concertos.

At larger scales still, solar systems are completely describable with computers, although the mathematics becomes difficult, and as we move out into galaxies and the entire universe the descriptions become difficult again.

Changing scales thus involves the successive movement in and out of simplicity. Where is the complexity in the universe greatest? It turns out to be at about one meter. In other words, at our scale. A great spike in complexity appears just where we and other forms of life arose.

That is no accident. A philosophical idea called the weak anthropic principle suggests that any part of the universe that can sit around and contemplate itself and the larger universe must itself be complex. We are constrained to live

at a scale of great complexity, or not to exist at all. That is worth some reflection.

But we try to find simplicity among this complexity, to let us feel we understand, and to let us predict what can happen.

## 2.3 What is a model?

Science strives for simplicity, and models are part of the process. What is a model? It is just a simplified view of something more complex.

The word “model” is used here essentially as it’s used in everyday English. For example, in ordinary English, “modeling clay” can be used to make simplified miniatures of three-dimensional images of animals, automobiles, buildings, or even full-scale three-dimensional images of objects like the human heart.

A “model airplane” can be rendered to show at a glance the physical appearance of a large aircraft, and can even be constructed to fly so as to test aerodynamics under proper rescaling. A “model organism” is a simpler organism that may respond to medical tests or treatments in ways similar to those of a more complex organism.

Even the fashion model on the runway meets this definition of a simplified view of something more complex. The infinite complexity of the human spirit is not relevant on the runway; all that is relevant in this context is the person as a realistic way to display fashions.

This book focuses on computational and mathematical models of ecological systems. What is left out of these models is as important as what is put in. Simplification is key.

If you have a complex natural system you don't understand, and you construct a computer model incorporating everything you can about that natural system, you now have two systems you don't understand. —after Chris Payola, UMN

A designer knows he has achieved perfection not when there is nothing left to add, but when there is nothing left to take away. —Antoine de Saint-Exupery

Two different simplifications of time are commonly used in ecological models:

- *Discrete time*★—Events happen at periodic time steps, as if time is non-existent in between.
- *Continuous time*★—Events happen smoothly and at all times.

In addition, there are two different classes of models:

- *Macroscale*★—Individual organisms are not tracked, but are measured in aggregate and represented by composite variables such as  $N$ .
- *Microscale*★—Individual organisms are tracked separately. These are also known as agent-based or individual-based models.

Macroscale models can be handled either by computers or mathematics, but microscale models are usually restricted to computers. Keep in mind that all four categories are only approximations of reality.

Later in this book we will also explore mechanistic versus phenomenological models.



## 2.4 Present state

As a surprising side note, the standard models commonly taught in ecology courses are not complete, and a main purpose of this book is to help make them more so. One aspect of theory related to simple species, for instance—called orthologistic population growth—is rarely even studied, much less taught, yet is essential for understanding rapidly growing populations, including human populations in millennia past. For two-species interactions, another theory concerning mutualisms and a related kind of population growth is highly under-developed, and the theory of three-species interactions is even less complete.



**Figure 2.2.** *The eternal mystery of the universe is its comprehensibility. —A. Einstein*

## **Chapter 3**

### **A basic population model**

#### **3.1 Characterizing populations**

One way to describe populations is to look at how many individuals they contain at various times. Or, instead of individuals, it may be more reasonable to consider total biomass—the total weight of all individuals in the population combined. For example, the number of trees may not be as important as their total weight, or the total area of their canopy. Density may also be relevant—how many individuals occupy a unit of area, or the percentage covered by the population in an area. All of these are gross properties of populations that can enter models.

Additional properties that can be taken into account include the age structure—the portions of the population of various ages, and the size structure—the portions of the population of various sizes. Such detail can be important because juveniles or older individuals may not reproduce. Genetic structure can also be important; it is often left out of ecological models, but evolutionary directions can affect the ecology as well.

Another important measure is the rate of change—how fast the population is changing. A population can be constant, increasing, or decreasing, or can fluctuate in complex ways.

Remember that a model is just a simpler view of something complex, and that all scientific models are just approximations of nature. When the full complexity cannot be understood, which is almost always, we can try to construct a simplified model in hopes of finding the essence.

## 3.2 Bacterial growth

The place to start a discussion of basic population models is in discrete-time at the macroscale—the most basic. Consider a hypothetical strain of bacteria reproducing every hour. Suppose a colony is started with a single bacterium when the clock reads zero, symbolized  $t = 0$ , and one hour later that bacterium divides into two, by time  $t = 1$ . Each of those divides in two one hour after that, by time  $t = 2$ . And so forth. Suppose you start this culture on a lab bench on Monday, let it go unchecked, and then come back late on Friday to see the results.

If the colony grows unchecked in this way, how many bacteria will there be at the end of the work week, after five full days of growth? You could figure that out on a calculator, or more easily you could use computer code. More easily, that is, once you know computer coding.

Because computer coding is becoming embedded in almost every aspect of life, appreciating the basics of coding is meaningful for each educated citizen of this century, and this book will expose you to the basics.

### 3.3 A first computer model

Below are two lines of computer code forming a program that models the bacterial colony as it doubles every hour. If you have not seen computer code before, don't be frightened by this; we will go through it carefully below.

```
N=1; t=0;
while(t<=5*24) { print(N); N=N*2; t=t+1; }
```

The above program is written in a generic programming language—it could be run as the programming language  $\mathcal{R}$ ,★ as the language AWK,★ or, with minor adjustments as the language C,★ Java,★ or a number of others. This particular code is essentially identical in many languages.

The first “statement” is `N=1`. That instructs the computer to set the number of bacteria, `N`, equal to 1. A semicolon (`;`) ends the statement and separates it from subsequent statements. The next statement is `t=0`. That instructs the computer to set the time `t` to 0. One bacterium at time zero forms the “initial conditions,” and once the computer has finished that line, the program is said to be “initialized.”

The second line of the program is more involved, but can be understood in two parts. The first part on the left, `while(t<=5*24)`, instructs the computer to repeat a set of code for 5 simulated days of 24 hours each. The second part is the code to be repeated, within braces on the right, `{...}`.

Considering the first part, `while` is a “keyword” that instructs the computer to repeat something until the “condition” in parentheses is no longer true. In this case, inside the parentheses is `t<=5*24`, which itself consists of three parts,

`t`, `<=`, and `5*24`. The first part, `t`, represents the time, which has just been initialized to zero in the previous line of code. The second part, `<=`, is the symbol for “less than or equal to.” Six such “comparison” symbols are possible, `==`, `<`, `<=`, `>`, `>=`, and `!=`, representing comparison for equal, less than, less than or equal, greater than, greater than or equal, and not equal, respectively. In the third part, the asterisk (`*`) is a symbol for multiplication, so `5*24` means “five times twenty-four,” a way to represent the number 120, or the number of hours from Monday to Friday—the amount of time the hypothesized bacterial culture is to reproduce.

Computer coding is an exacting business, where tiny variations can make huge differences. The computer is the ultimate literal interpreter. An example of this just slipped by in the previous paragraph. In coding, a single equals sign, `=`, means “change something to be equal to,” whereas two consecutive equals signs, `==`, means “compare to see if two things are the same.”

If you are accustomed to coding, you will already be familiar with such subtleties; if this is all new to you, it is something to get used to. Various [primers](#) on the web can help, but don’t be discouraged if it seems difficult at first; computer coding turns out to be one of the easiest things to jump into but one of the most difficult areas of all human endeavour to get exactly right. Time and patience will assist.

Getting back to the code, the phrase `while(t<=5*24)` means, in this case, to repeat something as long as the time, `t`, is less than or equal to 120 hours, 5 times 24. And that something to be repeated appears within braces to the right,

`{...}`. (By the way, many programming languages use three main symbols for grouping information—called braces, `{ }`, brackets, `[ ]`, and parentheses, `( )`. They are used for various kinds of groupings, but unfortunately their usage is not consistent across all languages.)

The first statement within braces is `print(N)`. (Refer back to the two-line program on page 20.) “Print” is a term left from the days when computers would communicate largely by printing on paper. Now the term just means “display.” The statement thus means “display the number of individuals in the population, `N`, at this time.” That was set to 1 in the previous line, so when the computer runs `print(N)` for the first time, it will display the number 1, typically on your screen.

The next statement, `N=N*2`, is read “`N` equals `N` times two.” It is similar in form to the statement on the first line, `N=1`, which started things off with a single bacterium. The ‘`N=`’ part is the same. It tells the computer that the number of bacteria, `N`, is about to change. (Of course, the computer has no clue what the program is about—that you are running a program about bacteria.) What `N` will change to is immediately to the right of the equal sign, `N*2`. The asterisk (`*`) means multiply. So this statement thus tells the computer to double the value of `N`. That is what the hypothesized bacterial population does every hour, so this statement models that doubling.

The third statement on the line, `t=t+1`, is read “`t` equals `t` plus one.” It is similar in form to the statement on the first line, `t=0`, which started things off with a clock time of zero.

In other words, in this example of letting bacteria grow for a five-day work week, we are taking midnight Monday morning to be hour zero. Five days later, at midnight Friday night, that becomes hour 120 (5 days times 24 hours per day equals 120 hours). So similarly,  $t=$  tells the computer that time  $t$  is about change. Following the equals sign is what it should change to,  $t+1$ , or one more than what it is at the moment, which advances the time by one hour. This is a *discrete time* model, so it approximates the real system by modeling only specific moments.

Those three statements are run in order, from left to right, first displaying the number of bacteria, then modeling the doubling of the bacterial population, and then advancing to the next hour. By the way, it may have occurred to you that the last two statements could be written in either order, or even run at the same time—they are independent, so the ordering would not matter.

After all three statements are run, your display will contain the number 1,  $N$  will be 2, and  $t$  will be 1. The computer next examines the code inside the parentheses associated with the keyword **while** to see if the three statements inside the braces should be run again. That condition specifies that as long as the time  $t$  is less than or equal to 120, the three statements must be repeated. At this point,  $t$  is equal to 1, which certainly is less than 120. Therefore the three statements will be run again.

This is called a “loop,” and now the computer will begin the second time around the loop, running the three statements again as they ran before, but now with altered values



of  $N$  and  $t$ . First it will display  $N$ , which is now equal to 2, so it will display 2. Then it will double  $N$  again, changing it from 2 bacteria to 4, and increase the time  $t$  by 1, from hour 1 to hour 2.

Thus the process repeats. Examining the condition inside the parentheses, the computer finds that 2 is less than or equal to 120, and so the three statements inside braces are run again. This goes on and on until  $t$  is greater than 120, at which time the loop is finished. At the end,  $t$  will be 121 and  $N$  will be whatever number has been reached by the process of doubling.

This code illustrates two fundamental aspects of computer coding: “condition testing” and “looping.” In larger programs loops are “nested” within other loops and condition tests are nested correspondingly. But this two-line program, with the first line initializing and the second line running a loop, is sufficient for our first model. You will soon see that this is not a trivial model, but one that demonstrates an inviolable law of biology, which Darwin put directly to use in creating his theory of evolution.

### 3.4 Program results

Here is what the program produces, shortened to fit on a page of this book.

```
1
2
4
8
16
32
:
6.64614 × 1035
1.32923 × 1036
```

If you run this program in  $\mathcal{R}$  or another suitable language, you should see something essentially identical to the above. Between Monday and Friday, 120 bacterial doublings would produce over  $10^{36}$  bacteria—that’s 1 followed by 36 zeros.

That is the computational result. The scientific question is how many individuals this amounts to. Worked out exactly, it is this number:  $2^{120} = 1,329,227,995,784,915,872,903,807,060,280,344,576$ . To understand the size of this number, suppose the bacteria are roughly cubical  $1\ \mu\text{m}$  on a side—one millionth of a meter, or about four hundred-thousandths of an inch (a suitable order-of-magnitude for a bacterium). What volume will the colony occupy in cubic meters at the end of the work week, after five full days of growing unchecked? You might want to speculate: will it fill the culture plate, overflow onto the lab bench, fill the lab, or what?

Work it out and you will see that the answer is  $2^{120}$  bacteria times  $10^{-18}$  cubic meters per bacterium equals about  $1.3 \times 10^{18}$  cubic meters total. How large is that? Estimate the ocean to be a film averaging 3.7 kilometers deep and coating two-thirds of a sphere with a 6400 kilometer radius (this approximates the amount of the earth's surface that is covered by ocean). This is about  $1.3 \times 10^{18}$  cubic meters! At the end of five days, the colony unchecked would thus fill all oceans of the earth with a dense microbial mass, from the greatest depths up to the surface!

This result has deep-reaching implications. First, even though this bacterial model can be quite accurate for a day or so, it fails completely over the course of a week. All models are approximations to reality, at best applicable over a suitable range. Second, there are lessons in its failure. It illustrates one of the inviolable laws of biology—that no population growth can remain unlimited for long. And third, in a mind like Charles Darwin's, and coupled with other biological principles, it leads to the conclusion that organisms must evolve. That is the story of Darwin's elephants.

### 3.5 Darwin's elephants

With elephants recognized as the slowest breeders of all known animals, Darwin made a laborious calculation, similar to the bacterial calculation above but more detailed, assuming that elephants started breeding at age 30 and continued until age 90, producing 6 young in that time.



**Figure 3.1.** Elephants and Kilimanjaro.

Of course he had no computers, nor calculators, and apparently kept track of 90 or more age classes and made his calculations (which have never been found) on paper. He calculated by hand on paper and alas those notes have never been found. But he said it cost him “some pain” to reach the conclusion that at the end of the fifth century, fifteen million elephants would be walking the earth, descended from one original pair. From this, he concluded that unlimited growth is impossible.

There is no exception to the rule that every organic being naturally increases at so high a rate that, if not destroyed, the earth would soon be covered by the progeny. —*Charles Darwin, 1859*

**T**hat he explained in Chapter Three of his *Origin of Species*. After explaining results of selection by people in the breeding of domestic animals, he introduced the concept of selection by natural causes in the wild, which he called “natural selection.” The simplest model of unlimited population growth was thus useful in the extreme, leading to an inviolable law of biology and the theory of evolution as one of its consequences. Individuals with qualities that allow them to suffer lower mortality or to reproduce slightly faster, and who pass those qualities to their offspring, will be the ones whose qualities predominate.



**Figure 3.2.** *Charles Darwin was in his twenties when he realized that natural selection was a cause of evolution and started to formulate his theory.*

## Chapter 4

### Modeling a single population

#### 4.1 Density-independent growth

Density, in the sense of population density, refers to how many individuals are present on average per unit area. One could say, “The density of elk in Yellowstone National Park during the summer is about 3 to 6 per square mile.” Sometimes, however, you will see density used as the total number in a place. You may see, “The density of elk in Yellowstone National Park during the summer is about 10 to 20 thousand.” The symbol  $N$  is often used for population density.

In the first case above, you would write  $N = 4.5$ , the midpoint between 3 and 6. In the second case you would write  $N = 15000$ . It should be clear from context what the area is.

With this in mind, all of the following statements are equivalent:

1. The population doubles each hour. (As in the bacterial example of the previous chapter.)
2. The population  $N(t)$  doubles each hour.

Here the number of individuals is represented by the letter  $N$ , and  $N(t)$  means population at time  $t$ . In the bacterial example, there was one bacterium at the beginning of the experiment when the clock started running,

so you would write  $N(0) = 1$ . One hour later, the hypothetical population had doubled, so you would write  $N(1) = 2$ . Doubling successively then gives  $N(2) = 4$ ,  $N(3) = 8$ , and so forth until after five days, or 120 hours,  $N(120) = 10^{36}$ , or slightly more—enough to fill all the oceans of the world.

3. The population  $N$  doubles each hour.

Often the “ $(t)$ ” is left off for simplicity, it being understood that the population  $N$  is a function of time.

4.  $N$  doubles each hour.

Since  $N$  represents a population in this case, the word “population” will often be dropped for conciseness.

5.  $N(t + 1) = 2 N(t)$ .

In English this would be read “ $N$  of  $t$  plus 1 equals two times  $N$  of  $t$ .” That simply means that the population at some time, anytime,  $t$ , when multiplied by 2, is the population in the next time step,  $t$  plus one.

6. The change in the population each hour is equal to the size of the population that hour.

This may sound pretty confusing. But it means that the amount that the population increases in the time step is equal in size to the whole population. Usually the increase is much less than that, perhaps a few percent, but here we are dealing with a rapidly increasing bacterial population.

7. The change in the population each hour is  $N(t+1)$  minus  $N(t)$ , which is to say  $N(t+1) - N(t) = 2 N(t) - N(t) = N(t)$ .



Here the population in the next hour,  $N(t+1)$ , minus the population now,  $N(t)$ , which is the change in population, is twice the current population,  $2N(t)$ , minus the current population,  $N(t)$  (not less confusing, perhaps).

8. The change in the population each hour, call it “Delta  $N$ ” or  $\Delta N$ , is  $\Delta N/\Delta t = 2N(t) - N(t) = N(t)$ .

Here the symbol delta ( $\Delta$ ) means *change in* or the *difference*. So  $\Delta N$  means the change in  $N$ , and  $\Delta t$  means the change in  $t$ . So the change in  $N$  per unit of time is written  $\Delta N/\Delta t$ , where delta  $t$  is the time unit being used, such as hour or day. This statement is thus the same as the previous one, but with symbols to shorten it.

9.  $\Delta N/\Delta t = N$ .

This means the population change in each time unit is equal to the population size itself. That is just because the population is doubling each time step.

10.  $\frac{1}{N} \frac{\Delta N}{\Delta t} = 1$ .

This is just dividing both sides of the previous equation by  $N$ , and perhaps looks even more confusing. However, in what follows, it turns out to be the most useful of all.

To move forward, let's focus on the last equation, with its parts colored in the box below.

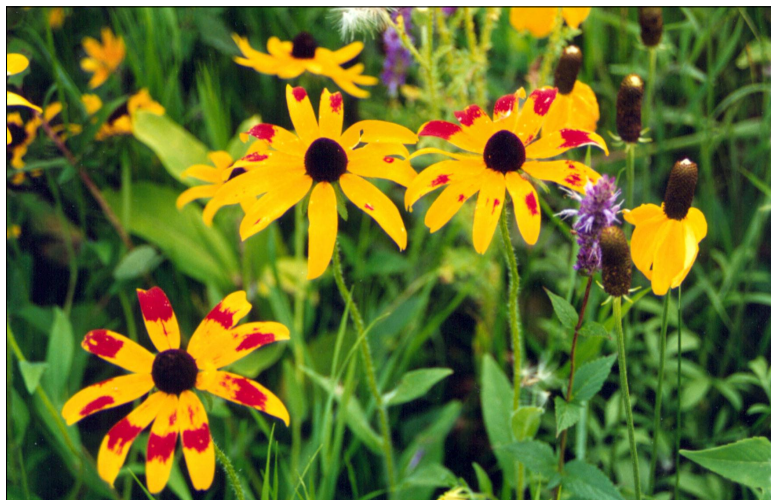
$$\frac{1}{N} \frac{\Delta N}{\Delta t} = 1 \quad \text{There is one new individual ...}$$

$$\frac{1}{N} \frac{\Delta N}{\Delta t} = 1 \quad \text{every hour ...}$$

$$\frac{1}{N} \frac{\Delta N}{\Delta t} = 1 \quad \text{for every member of the population.}$$

In the first row, the “ $\Delta N = 1$ ” refers to a change in the population of one individual, because delta ( $\Delta$ ) means change. In the second row, the “ $\Delta t$ ” in the denominator modifies this to the change in each time step—in this, case each hour. In the third row, the  $1/N$  modifies it drastically to mean the change in the population *per individual* in the population.

This could mean that one new individual is born while the parent lives on, or that two new individuals are born and the parent dies, or that the parent divides in two, or other equivalent events. In this model, these details are abstractions that do not matter for purposes of projecting the population. The model simply records the number of offspring produced by each member of the population and surviving to reproduce. Multiplied by 100, this becomes the percentage growth of the population. For humans, this is like the number of children



**Figure 4.1.** Wild *Rudbeckia hirta* with an unusual stroke of red boldly bisecting its petals.

per family who survive to adulthood. (Though it has to be divided by two if there are two parents per family.)

You have seen how rapidly that blows up, from the calculation on page [25](#).

## 4.2 Density-enhanced growth

Darwin made unparalleled use of a model that failed, but how can the model be improved so that it does not fail?

Think of only three Black-Eyed Susan plants (*Rudbeckia hirta*) becoming established in Yellowstone National Park, one near the north-east entrance, one in the center, and a third near the south entrance—the plants thus separated by over 30 miles. How often would the same pollinator be able to visit two of the plants so the plants could reproduce? Rarely or never, because these pollinators travel limited distances. The plant's growth rate will thus be 0. (In fact, it will be negative, since the three plants will eventually die.)

Suppose instead that 1000 of these plants were scattered about the park, making them about 2 miles apart. Occasionally a pollinator might happen by, though the chance of it visiting one of the other Black-Eyed Susans would be very low. Still, with 1000 plants in the area, the growth rate could be slightly positive.

Now consider 1,000,000 of those plants, making them about 100 meters apart. Pollination would now become relatively frequent. The growth rate of the population thus depends on the number of plants in the vicinity, meaning that this number must be part of the equation used to calculate the population growth rate.

We can use the equation introduced earlier to calculate this rate. First, put a parameter in place of the 1, like this.

$$\frac{1}{N} \frac{\Delta N}{\Delta t} = r, \text{ where } r \text{ formerly was } 1$$

Then attach a term that recognises the density of other members of the population,  $N$ .

$$\frac{1}{N} \frac{\Delta N}{\Delta t} = r + sN$$

Here  $r$  is related to the number of offspring each plant will produce if it is alone in the world or in the area, and  $s$  is the number of additional offspring it will produce for each additional plant that appears in its vicinity.

Suppose  $r = 0$  and  $s = 1/20$ , just for illustration, and start with three plants, so  $N(0) = 3$ . That is

$$\frac{1}{N} \frac{\Delta N}{\Delta t} = 0 + 0.05N$$

For watching the dynamics of this, multiply it out again

$$\frac{\Delta N}{\Delta t} = (0 + 0.05N) N$$

and convert the model to computer code, like this.

```
r=0; s=0.05; dt=1; t=0; N=3; print(N);
while(t<=14)
{ dN=(r+s*N)*N*dt; N=N+dN; t=t+dt; print(N); }
```

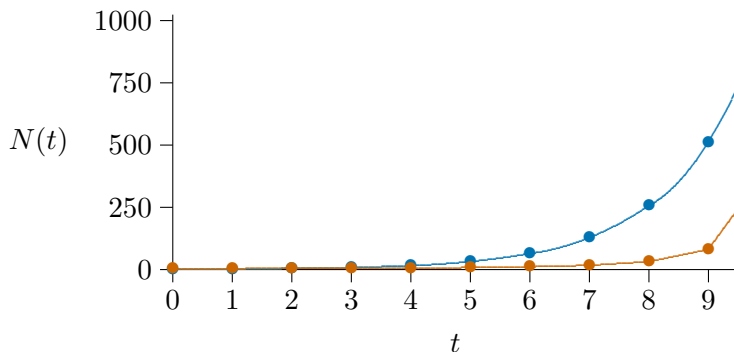
If you run this model in  $\mathcal{R}$  (or other languages in which this code works, like C or AWK), you will see the numbers below.

```

3
3.45
4.045125
4.863277
6.045850
7.873465
10.97304
16.99341
31.43222
80.83145
407.5176
8,711.049
3,802,830
723,079,533,905
26,142,200,000,000,000,000,000

```

Graph these, and you will see the numbers expand past all bounds, vertically off the page.



**Figure 4.2.** Orthologistic growth (red) contrasted with exponential growth (blue).

The blue line shows the unlimited bacterial growth (exponential growth) that helped lead Darwin to his idea of natural selection. The red line illustrates the new “density-enhanced growth” just being considered, where growth rate increases with density.

Because it approaches a line that is orthogonal to the line approached by the logistic model, described later, we call this an “orthologistic model.” It runs away to infinity so quickly that it essentially gets there in a finite amount of time. In physics and mathematics this situation is called a “singularity”—a place where the rules break down. To understand this, it is important to remember that all models are simplifications and therefore approximations, and apply in their specific range. The orthologistic model applies well at low densities, where greater densities mean greater growth. But a different model will take over when the densities get too high. In fact, if a population is following an orthologistic model, the model predicts that there will be some great change that will occur in the near future—before the time of the singularity.

In physics, models with singularities command special attention, for they can reveal previously unknown phenomena. Black holes are one example, while a more mundane one from physics is familiar to all. Consider a spinning coin with one point touching the table, spinning ever more rapidly as friction and gravity compel the angle between the coin and the table to shrink with time. It turns out that the physical equations that quite accurately model this spinning coin include a singularity—a place where the spinning of the coin becomes

infinitely fast at a definite calculable time. Of course, the spinning cannot actually become infinitely fast. As the coin gets too close to the singularity—as its angle dips too near the table—it merely switches to a different model. That different model is a stationary coin. The exact nature of the transition between the spinning and stationary states is complex and debated, but the inevitability of the transition is not.

It is no different in ecology. Reasonable models leading to singularities are not to be discounted, but rather considered admissible where they apply. They arise inescapably in human population growth, considered in the next chapter.

### 4.3 Density-limited growth

What about outside of the range of the orthologistic model? Think of the same Black-Eyed Susans, not only close enough that pollinators can flit fluently from one to another, but also crowded so that they start to shade one another, and their roots start to compete for water and nutrients. What is a suitable model for this?

The growth rate will again depend on the number of plants, but now more plants will *reduce* the growth rate. That just means a minus sign on  $s$ .

$$\frac{1}{N} \frac{\Delta N}{\Delta t} = r + sN, \quad s < 0$$

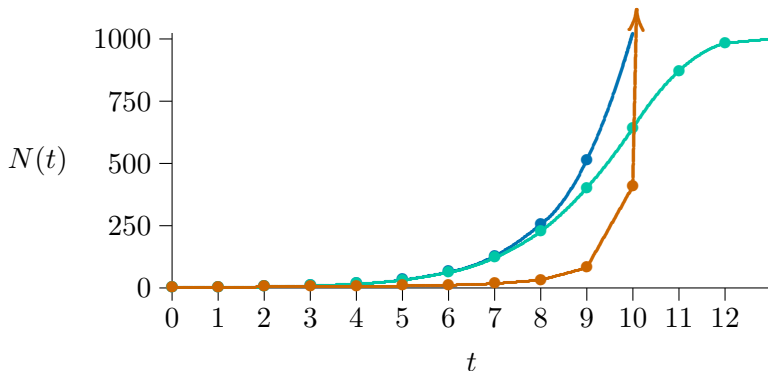
Again,  $r$  is the number of offspring each will produce if it is alone in the world, but with  $s$  negative,  $s$  is the number each plant will be *unable to produce* for each additional plant that appears in its vicinity.



Suppose we have  $r = 1$  and  $s = -1/1000$ , and we start with three plants, so  $N(0) = 3$ . Here is the code, with the new negative  $s$  in red.

```
r=1; s=-0.001; dt=1; t=0; N=3; print(N);
while(t<=20)
{ dN=(r+s*N)*N*dt; N=N+dN; t=t+dt; print(N); }
```

Now, because  $s$  is negative, the growth rate  $1/N \Delta N / \Delta t$  will drop as the population increases, so you might surmise that the rate will eventually reach zero and the population will level off. In fact, it levels off to 1000.



**Figure 4.3.** Logistic growth (green) contrasted with orthologistic growth (red) and exponential growth (blue).

The value at which it levels off is called an “equilibrium,” a value where the dynamical system becomes quiescent and stops changing. In the case of the logistic equation, it is also called the “carrying capacity,” a level at which the environment cannot “carry” any larger population.

But why 1000? What value of  $1/N \Delta N/\Delta t$  will make the population level off? When  $\Delta N$  is 0, that means “the change in  $N$  is zero.” And that means  $N$  stops growing. And when  $\Delta N$  is zero, the entire term on the left is zero and algebra proceeds as follows.

$$\begin{aligned}\frac{1}{N} \frac{\Delta N}{\Delta t} &= r + sN \\ 0 &= r + sN \\ -sN &= r \\ N &= -r/s\end{aligned}$$

So the carrying capacity is  $-r/s$ . In Figure 4.3,  $-r/s = -1/(-0.001) = 1000$ . Exactly where it ended up!

This is the celebrated “logistic equation,” published in 1838 by Pierre Verhulst.★ It is commonly written

$$\frac{\Delta N}{\Delta t} = r N \left( 1 - \frac{N}{K} \right)$$

Notice that when  $N$  is equal to  $K$ , the factor in parentheses on the right becomes  $1 - N/N = 1 - 1 = 0$ , so the whole growth term  $\Delta N/\Delta t$  becomes zero and the population stops growing. Thus  $K$  is carrying capacity, and therefore  $K = -r/s$ .

As an exercise, you might want substitute  $-r/s$  for  $K$  in the equation above, then simplify and see if you get the  $r + sN$  formulation.

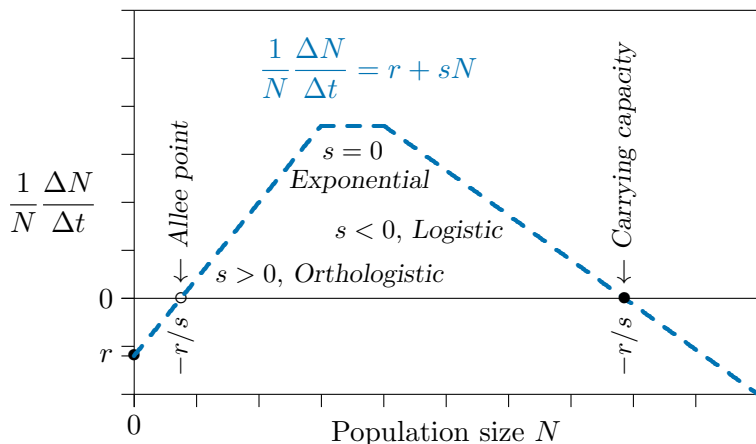
## 4.4 Parameter combinations

Before moving further, consider all possible combinations of the parameters, as determined by their signs. There are six possibilities, ignoring growth rates of exactly zero as infinitely unlikely.

1.  $r > 0, s > 0$  Orthologistic growth.
2.  $r < 0, s > 0$  Orthologistic growth with an Allee point.
3.  $r > 0, s = 0$  Exponential growth.
4.  $r > 0, s < 0$  Logistic growth with a carrying capacity.
5.  $r < 0, s < 0$  Inviabile population declining to extinction.
6.  $r < 0, s = 0$  Same as above.

Figure 4.4 shows three of these possibilities pieced together to form a complete population model. On the left in the figure, number 2 above, orthologistic growth with an Allee point,<sup>★</sup> prevails at low densities, where larger numbers of other members of the species in the vicinity enhance growth. In the middle, number 3 above, exponential growth, occurs as a transition phase. Finally on the right, number 4 above, logistic growth with a carrying capacity, takes over when crowding and other limitations reduce growth rates as larger numbers of other members of the species in the vicinity appear.

The vertical axis in Figure 4.4 shows the individual growth Rate, and the horizontal axis shows the population density. On the right, where the slope is negative, as the density approaches  $-r/s$  from the left the growth rate on the vertical axis drops to zero, so the population stops growing.



**Figure 4.4.** A general population growth model can be assembled from piecewise linear components.

This is the equilibrium value called the “carrying capacity.” If something pushes the population above that value—immigration of animals from another region, for example—then the growth rate on the vertical axis drops *below* zero. The growth rate then is negative, and therefore the population declines. On the other hand, if something drops the population below that value—such as emigration of animals to another place—the growth rate on the vertical axis rises *above* zero. That growth rate is positive, and therefore the population grows.

The carrying capacity is “stable.” A value is said to be stable if it tends to restore itself when it is pushed away by some outside force.

The situation is entirely different on the left in the figure, where the slope is positive. As on the right, when the density is  $-r/s$ , the growth rate on the vertical axis reaches



zero, meaning the population does not change. This is an equilibrium too—not a carrying capacity, but an Allee point.★ However, if the population here drifts below  $-r/s$ , the growth rate on the vertical axis becomes negative and the population declines further still. It is unstable. In this model the popu-

lation continues to decline until eventual extinction. Above the Allee point, however, the growth rate on the vertical axis is positive, so the population increases until it reaches some other limitation.

A species thus becomes endangered when its population drops below its Allee point, and if it is to be saved something must be done to change that point. The parameter  $r$  must somehow be increased—by restoring habitat, reducing predation by humans, or using artificial reintroductions or other conservation programs (e.g., Figure 4.5).

## 4.5 Generalization

In summary, the macroscale model for population dynamics of a single species, in its simplest form, is

$$\frac{1}{N} \frac{\Delta N}{\Delta t} = r + sN \quad (4.1)$$

This is a straight-line form of a more general form presented by Hutchinson,★

$$\frac{1}{N} \frac{\Delta N}{\Delta t} = r + sN + s_2 N^2 + s_3 N^3 + s_4 N^4 + \dots \quad (4.2)$$

and of the most general form proposed by Kolomogorov,★ where  $f(N)$  can be any function of the population density  $N$ .

$$\frac{1}{N} \frac{\Delta N}{\Delta t} = f(N) \quad (4.3)$$

The higher-order terms in Equation 4.2 could refine population projections if there were enough data to determine them. They are not really needed, however, because straight-line parts can be pieced together to form a general population growth curve, as in Figure 4.4. And as human population growth in Figure 6.3 will show, a piecewise approach can more closely approximate the real situation.

Moreover, blending separate versions of Equation 4.1 can generalize to either the Hutchinson or Kolomorgov forms, 4.2 and 4.3, as you will see in Chapter 18.



**Figure 4.5.** *Trumpeter swans—the largest North America birds, with wingspans reaching ten feet—were nearing extinction until deliberate protection and reintroduction programs brought their  $r$  values back to viable levels.*

## Chapter 5

### Differential and difference forms

$$\frac{1}{N} \frac{\Delta N}{\Delta t} = r + sN \quad \leftarrow \text{Difference equation model}$$

$$\frac{1}{N} \frac{dN}{dt} = r + sN \quad \leftarrow \text{Differential equation model}$$

Recall that the delta sign ( $\Delta$ ) means *change in* or the *difference*. Compare the difference equation with the differential form, which uses the terminology  $dN$  and  $dt$ . These represent infinitesimally small time steps, corresponding to our common-sense perception of time as divisible ever more finely without limit. In differential equations populations change smoothly rather than in finite steps—growth approximating that of organisms that can reproduce at any time, such as bacterial or human populations.

It turns out that differential equations are harder for computers to solve than difference equations. Computers cannot make infinitely fine time steps, but have to approximate by using very small time steps instead. On the other hand, difference equations can be harder to solve mathematically.

r=1; s=-0.001; N=1; t=0;

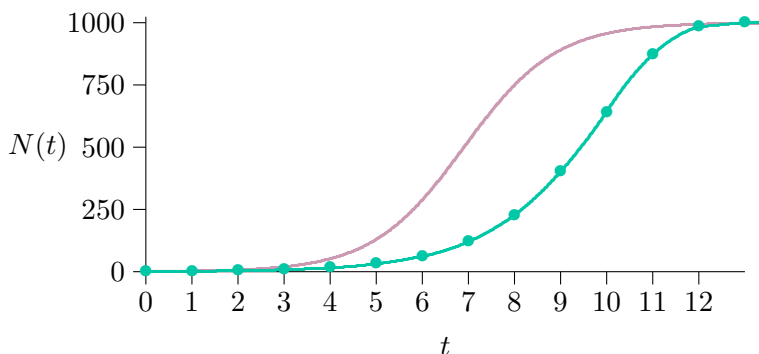


```
dt=1; print(N);  
while(t<=20)  
{ dN=(r+s*N)*N; N=N+dN; if(N<0) N=0;  
  t=t+dt; print(N); }
```

Above is computer code for a difference equation presented earlier, which levelled off at 1000, but with an addition in red. If the population is far above its carrying capacity, the calculation could show such a strong decline that the next year's population would be negative—meaning that the population would die out completely. The addition in red just avoids projecting negative populations. Below is similar code for the corresponding *differential* equation, with the differences again in red.

```
r=1; s=-0.001; N=1; t=0;  
dt=1/(365*24*60*60); print(N);  
while(t<=20/dt)  
{ dN=(r+s*N)*N*dt; N=N+dN; if(N<0) N=0;  
  t=t+dt; print(N); }
```

This intends to model *infinitely small* time steps. Of course it cannot do that exactly, but must settle for *very small* time steps. Instead of  $dt = 1$ , for example, representing one year, it is set here to about one second, dividing 1 year by 365 days and each day by 24 hours, 60 minutes, and 60 seconds. This is hardly infinitely small, but for populations of bacteria and humans it is close enough for practical



**Figure 5.1.** Differential logistic growth (maroon) compared with discrete (green). No dots appear on the differential form, since that represents infinitesimal time steps, whereas the difference form has a dot at each point calculated.

purposes. Still, it is important to check for negative populations in case the time step is not small enough.

How small is close enough to infinitely small? is the question. To find out, you can set the time step to something small and run the code, which will produce a set of population values through time. Then set the step smaller still and run the code again. It will run more slowly because it is calculating more steps, but if essentially the same answer appears—if the answer “converges”—then you can make the step larger again, speeding the calculation. With a few trials you can find a time step that is small enough to give accurate answers but large enough to allow your code to run reasonably fast.

Figure 5.1 shows the results of running the differential equation version of the program (the second one above, in maroon) versus the difference equation version (the first above, in green). The differential equation has the same parameters and general shape, but the population approaches its carrying capacity more quickly. Because the differential time steps produce offspring earlier—not waiting for the end of the step—offspring are available to reproduce earlier, and so forth.

This particular method for differential equations is called “Euler’s method” (pronounced “Oiler’s”), a basic approach not often used in the twentieth century because computers not so long ago were millions of times slower than they are now. Today this method is often fast enough, and is desirable because of its relative simplicity.

(By the way, calculating bacterial growth for five days with one-second time steps will be fast enough in any programming language. At the time we are writing this (second decade of the twenty-first century), calculating growth for a human population, second-by-second for 20 years, doing the same for 20 years second by second for humans will be too slow in  $\mathcal{R}$ , tolerable in AWK, and plenty fast in C, Java, or other high-speed languages.)

## 5.1 A mathematical view

Differential equations can be amenable to mathematical analysis. To repeat, here is the differential population model.

$$\frac{1}{N} \frac{dN}{dt} = r + sN \quad (5.1)$$

It turns out there is something simple about infinity, and when time steps are infinitely small the methods of calculus developed over the centuries can solve this differential equation exactly, mathematically. If you apply a symbolic mathematics computer package, or the methods for integration of functions developed in calculus, you can find the population value  $N$  for any future time  $t$ . This is called the “solution” to the differential equation.

$$N(t) = \frac{1}{\left(\frac{s}{r} + \frac{1}{N_0}\right) e^{-rt} - \frac{s}{r}} \quad (5.2)$$

Most differential equations cannot be solved this way but, fortunately, the basic equations of ecology can. This solution becomes useful in projecting forward or otherwise understanding the behavior of a population. If you know the starting  $N$ ,  $s$ , and  $r$ , you can plug them into the formula to find the population size at every time in the future, without stepping through the differential equation.

## 5.2 Exponential solution

To think about this mathematically, first set  $s$  to zero, meaning no density dependence. The differential equation then reduces to  $dN/dt = r$ , and if you replace  $s$  in the equation above with 0 you get this:

$$\begin{aligned} N(t) &= \frac{1}{\left(\frac{0}{r} + \frac{1}{N_0}\right) e^{-rt} - \frac{0}{r}} \\ &= \frac{1}{\frac{1}{N_0} e^{-rt}} \\ &= N_0 e^{rt} \end{aligned}$$

A measure often used for exponential growth, and that we will apply later in this book, is “doubling time”—the time that must elapse for the population to double. For exponential growth, this is always the same, no matter how large or small the population. For exponential growth, the equation above is

$$N(t) = N_0 e^{rt} \tag{5.3}$$

$N_0$  is the starting population at time 0,  $N(t)$  is the population at any time  $t$ , and  $r$  is the constant growth rate—the “intrinsic rate of natural increase.” How much time,  $\tau$ , will elapse before the population doubles? At some time  $t$ , the

population will be  $N(t)$ , and at the later time  $t + \tau$ , the population will be  $N(t + \tau)$ . The question to be answered is this: for what  $\tau$  will the ratio of those two populations be 2?

$$\frac{N(t + \tau)}{N(t)} = 2$$

Substituting the right-hand side of Equation 5.3 gives

$$\frac{N_0 e^{r(t+\tau)}}{N_0 e^{rt}} = 2$$

The factor  $N_0$  cancels out, and taking natural logarithms of both sides gives

$$\ln \frac{e^{r(t+\tau)}}{e^{rt}} = \ln 2$$

Since the log of a ratio is the difference of the logs, this yields

$$\ln e^{r(t+\tau)} - \ln e^{rt} = \ln 2$$

Since logarithms and exponentials are inverse processes—each one undoes the other—the natural logarithm of  $e^x$  is simply  $x$ . That gives

$$r(t + \tau) - rt = \ln 2$$

$$r\tau = \ln 2$$

and finally, the doubling time  $\tau$  is

$$\tau = \frac{\ln 2}{r} \tag{5.4}$$

In other words, the doubling time for exponential growth, where  $r$  is positive and  $s$  is 0, is just the natural logarithm of 2 (0.69314718...) divided by the growth rate  $r$ .

### 5.3 Logistic solution

Recall that the carrying capacity is  $-r/s$ , also called  $K$ . So wherever  $-r/s$  appears, substitute  $K$ , as follows.

$$\begin{aligned} N(t) &= \frac{1}{\left(\frac{s}{r} + \frac{1}{N_0}\right) e^{-rt} - \frac{s}{r}} \\ &= \frac{1}{\left(-\frac{1}{K} + \frac{1}{N_0}\right) e^{-rt} + \frac{1}{K}} \\ &= \frac{K}{\left(-1 + \frac{K}{N_0}\right) e^{-rt} + 1} \\ &= \frac{K}{\left(\frac{K - N_0}{N_0}\right) e^{-rt} + 1} \end{aligned}$$

This is the solution given in textbooks for logistic growth. There are slight variations in ways it is written, but they are equivalent.

## 5.4 Orthologistic solution

Finally, let  $s$  be positive. This creates a vertical asymptote and orthologistic growth. The position in time of the vertical asymptote is the “singularity” mentioned earlier. The interesting question is, when  $s$  is positive, what is the time of the singularity? That is, when will the population grow beyond all bounds in this model?

What must happen to the denominator for the population to grow to unbounded values? It has to get closer and closer to zero, for then the  $N(t)$  will grow closer and closer to infinity. So to find the singularity, you only have to set the denominator to zero, and then solve for the time  $t$ . You can go through the intermediate steps in the algebra below, or use a mathematical equation solver on your computer to do it for you.

Setting the denominator in Equation 5.2 to zero will lead along this algebraic path:

$$\frac{s}{r} = \left( \frac{s}{r} + \frac{1}{N_0} \right) e^{-rt}$$

Multiply through by  $(r/s) e^{rt}$ , to obtain

$$e^{rt} = \left( 1 + \frac{r}{s} \frac{1}{N_0} \right)$$

Next take logarithms of both sides

$$r t = \ln \left( 1 + \frac{r}{s} \frac{1}{N_0} \right)$$



Finally, divide through by  $r$  to find the time of the singularity.

$$t = \frac{1}{r} \ln \left( 1 + \frac{r}{s} \frac{1}{N_0} \right)$$

In the 1960s, Heinz von Foerster★ wrote about this in the journal *Science*. Though the consequences he suggested were deadly serious, his work was not taken very seriously at the time, perhaps in part because the time was so far away (about a human lifetime), but perhaps also because he put the date of the singularity on Friday the 13th, 2026, his 115th birthday. In the title of his paper he called this “doomsday”, when the human population would have demolished itself.

Von Foerster used a more complicated model than the  $r+sN$  model we are using, but it led to the same result. Some of the ideas were picked up by Paul Ehrlich★ and others, and became the late-1960s concept of the “population bomb”—which was taken seriously by many.

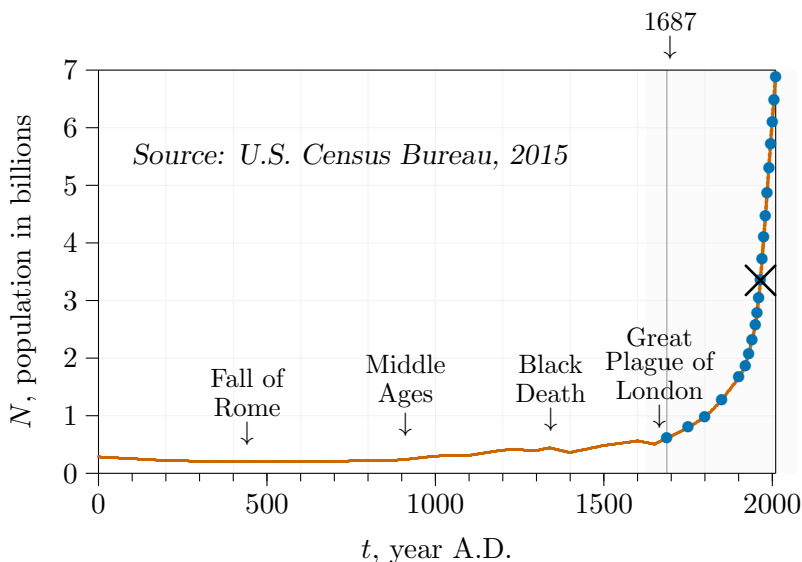
## Chapter 6

### Human population growth

There is a challenge for this chapter. Coming this far in the book you have learned a little about population growth, and you have access to computer coding, so you are ready for something big.

Imagine for fun that you have accepted a new job in Washington as a policy fellow with the United States Geological Survey, or USGS—one of the major research branches of the federal government. This is not farfetched; many recent doctoral graduates land such jobs at reasonably high levels. But suppose that your boss says she wants you to calculate what the world’s population will be in 2100. Other agencies have done this, but she wants a separate USGS estimate, presented in an understandable way. She can give you data from the 18th through the 21st centuries. She discloses that she is meeting with the Secretary General of the United Nations tomorrow and hopes you can figure it out today. You tell her “Sure, no problem.”

Are you crazy? No! The rest of this chapter will walk you through how to it. We’ll start by piecing together the parts, as in Figure 4.4—the orthologistic part, if there is one, and any exponential and logistic parts as well.



**Figure 6.1.** Global human population over the past 2000 years.

## 6.1 Phenomological graph

The excerpt of data you have been given includes the world's population in billions, by year. That is all. Figure 6.1 shows the data plotted in a phenomenological way— population size versus year, supplemented with a curve going back 2000 years to provide perspective. The blue dots show the range of data you will be using to project the future population, and the black 'x' marks a great demographic transition that

is not obvious in this graph, but that will become glaringly so in Figure 6.3.

Can you project global population by simply extending that curve? The population is clearly rising at an enormous rate, expanding most recently from 3 billion to 7 billion in less than half a century. Simply projecting the curve would lead to a prediction of more than 11 billion people by the middle of the 21th century, and more than 15 billion by the century's end.

But such an approach is too simplistic. In one sense, the data are all contained in that curve, but are obscured by the phenomena themselves. We need to extract the biology inherent in the changing growth rate  $r$  as well as the ecology inherent in the changing density dependence  $s$ . In other words, we want to look at data showing  $1/N \Delta N / \Delta t$  versus  $N$ , as in Figure 4.4.

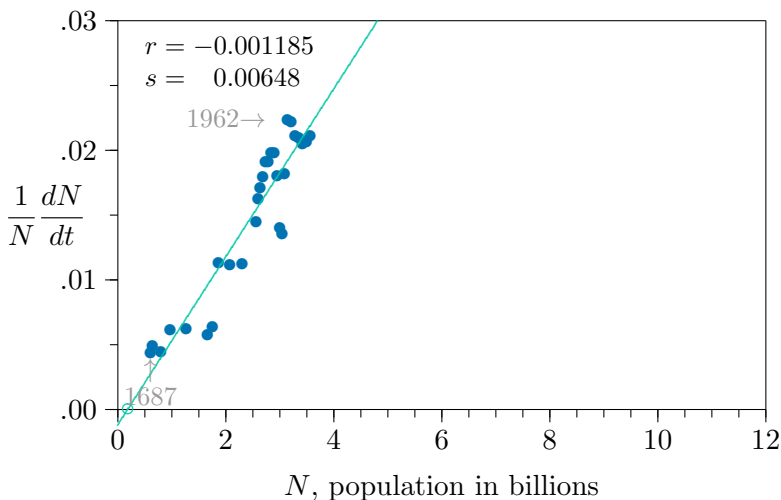
Table 6.1 shows a subset of the original data,  $t$  and  $N$ , plus calculated values for  $\Delta N$ ,  $\Delta t$ , and  $1/N \Delta N / \Delta t$ . In row 1, for example,  $\Delta N$  shows the change in  $N$  between row 1 and row 2:  $0.795 - 0.606 = 0.189$  billion. Likewise,  $\Delta t$  in row 1 shows how many years elapse before the time of row 2:  $1750 - 1687 = 63$  years. The final column in row 1 shows the value of  $1/N \Delta N / \Delta t$ :  $1/0.606 \times 0.189/63 = 0.004950495 \dots$ , which rounds to 0.0050. Row 21 has no deltas because it is the last row in the table.

**Table 6.1.** *Human population numbers for analysis.*

Point	Year $t$	$N$ billions	$\Delta N$	$\Delta t$	$\frac{1}{N} \frac{\Delta N}{\Delta t}$
1.	1687	0.606	0.189	63	0.0050
2.	1750	0.795	0.174	50	0.0044
3.	1800	0.969	0.296	50	0.0061
4.	1850	1.265	0.391	50	0.0062
5.	1900	1.656	0.204	20	0.0062
6.	1920	1.860	0.210	10	0.0113
7.	1930	2.070	0.230	10	0.0111
8.	1940	2.300	0.258	10	0.0112
9.	1950	2.558	0.224	5	0.0175
10.	1955	2.782	0.261	5	0.0188
11.	1960	3.043	0.307	5	0.0202
12.	1965	3.350	0.362	5	0.0216
13.	1970	3.712	0.377	5	0.0203
14.	1975	4.089	0.362	5	0.0177
15.	1980	4.451	0.405	5	0.0182
16.	1985	4.856	0.432	5	0.0178
17.	1990	5.288	0.412	5	0.0156
18.	1995	5.700	0.390	5	0.0137
19.	2000	6.090	0.384	5	0.0126
20.	2005	6.474	0.392	5	0.0121
21.	2010	6.866			

## 6.2 Biological–ecological graph

Figure 6.2 plots the two green columns of Table 6.1 through line 12—the mid-1960s—in blue dots, with a green line representing the average trend. A line like this can be drawn



**Figure 6.2.** Observed human growth rate as a function of population density through the mid-1960s (blue dots), based on the data from Table 6.1, with a line representing the average trend (green).

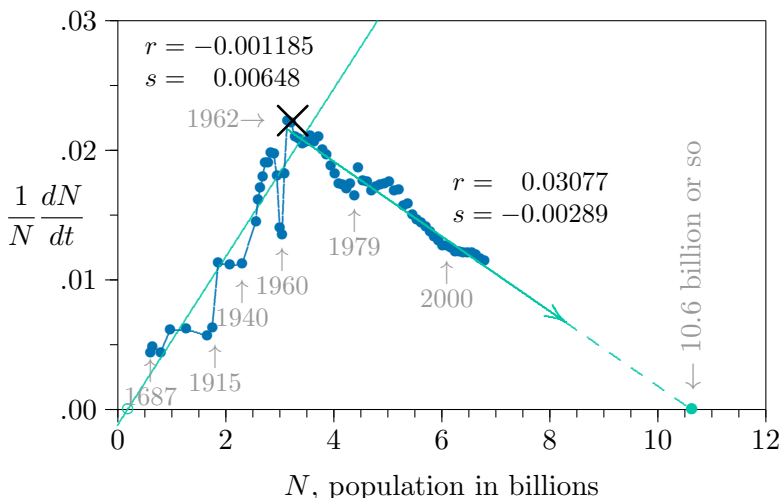
through the points in various ways—the simplest with a ruler and pen drawing what looks right. This one was done using a statistical “regression” program, with  $r$  the point at which the line intersects the vertical axis and  $s$  the line’s slope—its  $\Delta y/\Delta x$ . The intrinsic growth rate  $r$  for modern, global human population is apparently negative and the slope  $s$  is unmistakably positive.

From the late 1600s to the mid 1960s, then, it's clear that the birth rate per family was increasing as the population increased. Greater population was *enhancing* the population's growth. Such growth is orthologistic, meaning that the human population has been heading for a singularity for many centuries. The singularity is not a modern phenomenon, and could conceivably have been known before the 20th century.

The negative value of  $r$ , if it is real, means there is a human Allee point. If the population were to drop below the level of the intersection with the horizontal axis—in this projection, around two hundred million people—the human growth rate would be negative and human populations would decline. The Allee point demonstrates our reliance on a modern society; it suggests that we couldn't survive with our modern systems at low population levels—although perhaps if we went back to hunter-gatherer lifestyles, this would change the growth curve. The Allee point thus indicates that there is a minimum human population we must sustain to avoid extinction. We depend on each other.

### 6.3 A global transition

In Figure 6.3 we add data from the mid-1960s to the present day. People living in the 1960s were completely unaware of the great demographic transition that was developing. For hundreds of years prior to this time, human populations were stuck on an orthologistic path, with a singularity ever looming and guaranteed by the positive slope. In most of the world, however, the slope abruptly turned about and negative. Not all countries of the world turned about, but on



**Figure 6.3.** Continuation of Figure 6.2 to the present day.

average the world did. Humanity started down a logistic-like path.

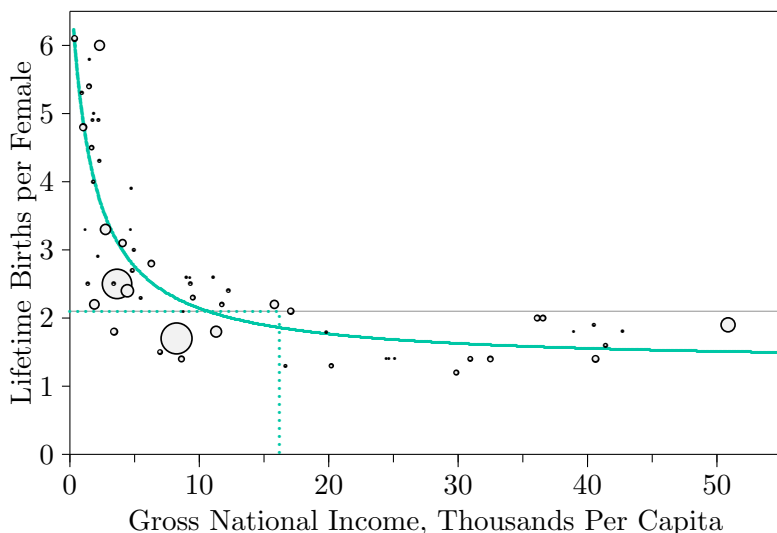
Where the downward-sloping line crosses the horizontal axis is where population growth would cease. From this simple  $r + sN$  model, it appears that world's population will stabilize between 10 and 12 billion. That is in line with other recently published projections.

Prior to the 1960s there were dips in the increasing growth, with World Wars I and II levelling the rate of increase worldwide, though population continued to grow rapidly. The rate



also fell in 1960, corresponding to extreme social disruptions in China.

What caused this great demographic transition, averaged over the globe? The “Four Horsemen” commonly expected to check human populations were not a primary cause. In many regions birth control, became more available. Education slowed reproduction because people got married later. Modern medicine raised survival rates, making large families unnecessary. The space program looked back at Earth and projected a fragile dot suspended in the black of space, viewed by billions. China’s one-child policy had a noticeable effect. However, so did HIV, one of the few Horsemen that has made a noticeable comeback.



**Figure 6.4.** *Human fecundity as a function of national per capita income.*

Plants and other animals have logistic growth forced upon them because of overcrowding. In humans, however, logistic growth has been largely voluntary. And there could be further developments in a lifetime. In many nations, birth rates are presently below replacement rates. In fact, in all nations with a gross national income above 16K dollars per person, the birth rate is at or below the replacement rate of 2.1 lifetime births per female (Figure 6.4).

This change in demographic rates could conceivably allow present and future generations to voluntarily adjust the population to whatever is desired. The new question just may be: what is the minimum world population we dare have?

Returning to your supervisor's questions, you can now tell her that, in 2100, the world's population will be between 10 and 12 billion. And you can say "The other population projections are not far off. They are slightly different from what we calculate using this method. But they use very complicated methods so you have to cut them a little slack!"



**Figure 6.5.** *Earth over Moon, touching the conscience of a world.*

## Chapter 7

### Chaos and randomness

In the density-limited growth examined thus far, the ecological effects of density fed back fast quickly enough that the population's growth could adjust and the population could reach a carrying capacity, equal to  $-r/s$ . But if the growth rate is too fast compared with that feedback, the population can overshoot its carrying capacity, which can lead to highly complex outcomes.

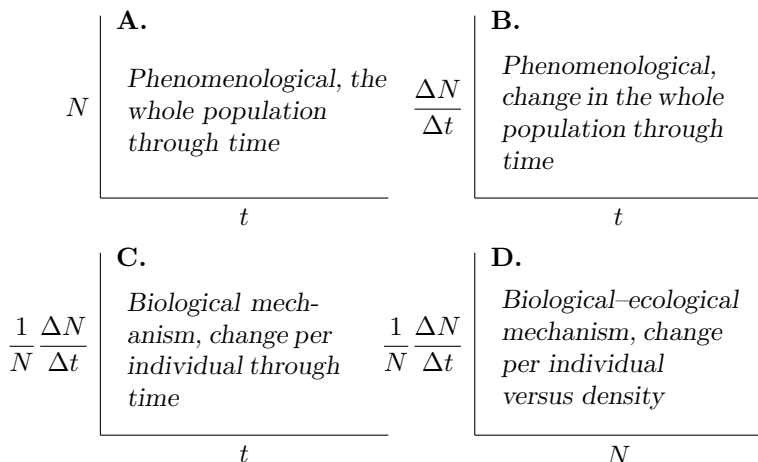
Think about feedback in this way. Imagine driving down the road, keeping your eye on the road, instantly correcting any little deviations of your car from your lane, adjusting the steering wheel without even perceiving it, and with only normal blinking of your eyes. In this case there is very little delay in your feedback to the steering wheel, and you stay in the lane. Now suppose you close your eyes for one second at a time, perhaps every ten seconds. (Do not run this experiment; just think about it!) You may have drifted a bit to the left or right in that second and would have to turn the steering wheel further to get back in you lane. And now imagine shutting your eyes for 15 seconds every minute, then opening them and correcting your path down the road. You'll start oscillating in your lane and precariously jerking back and forth, possibly visiting the ditch. The cause? The delay in the feedback between stimulus and response.

So it is with populations. Delays in sensing the carrying capacity can start oscillations. For example, a modelled insect population that grows and lays eggs one year and emerges the next year can suffer such oscillations. The insects are, in effect, “keeping their eyes shut” about how many insects will be produced the next year. This is in contrast to species like bacteria or humans, where the population grows more or less continuously.

## 7.1 Depicting population growth

Figure 7.1 shows four approaches to depicting populations. While not all equally helpful, each has its use. Let’s start with phenomenological graphs for a single species: graphs that merely depict the population phenomena observed without attempting to describe the mechanisms causing the phenomena. Observations might come from successive bacterial plate counts or censuses of people or, in this case, successive insect censuses. Part A in the figure represents the whole population  $N$  over time, and is a starting place to view population change. Similarly, Part B represents the whole population’s *rate* of growth,  $dN/dt$ , over time, also phenomenological.

A touch of biology is introduced in Part C by transforming the vertical axis to per-capita growth,  $1/N dN/dt$ . This transformation recognizes the growth rate that an individual organism achieves in a unit of time—say in a year or a week—under prevailing conditions. There is a nominal biological limit on the number of offspring produced by an



**Figure 7.1.** Population growth viewed four ways.  
(A,B) Phenomenological. (C,D) Mechanistic.

individual in each unit of time—one new bacterium per individual bacterium in twenty minutes, say, or four goslings per family of geese in a year, or one infant per human family each year. This subtle amount of biology can reveal patterns not evident in the phenomenological approaches of Parts A and B—that the number of surviving offspring per individual increases with time for orthologistic growth, does not change for exponential growth, and decreases with time for logistic growth.

Finally, in Part D, a touch of ecology is added to the biology of Part C by considering, on the horizontal axis, interactions among organisms. This shows per-capita growth rate versus population density  $N$ , rather than versus time  $t$ . And it reveals even more clearly the ecological mechanism behind the phenomena and the distinct nature of the three kinds of population growth—orthologistic growth appears as a straight line slanted upward (as in Figure 6.2), exponential growth as a straight horizontal line, and logistic growth as a straight line slanted downward (as in Figure 6.3). Population density  $N$  acts a proxy for space, food, or other resources or limits.

## 7.2 Hypothetical insect data

For a detailed illustration of the methods used in these four graphs and an illustration of population oscillations, consider the hypothetical insect data in Table 7.1. Insects often have one-year reproductive cycles; these can be prone to oscillations, and also are known for “outbreaks” (e.g. of disease, or of pests).

The data in Table 7.1 were generated by the difference equation  $1/N \Delta N / \Delta t = r + sN$ , with  $r = 3$  and  $s = -4$ . The table shows an initial population of about 11,000 individual organisms. The next year there are about 44,000, then 168,000, then more than 500,000, then more than 900,000. But then something apparently goes wrong, and the population drops to just over 55,000. In nature this might be attributed to harsh environmental conditions—a drastic change in weather or over-exploitation of the environment. But these

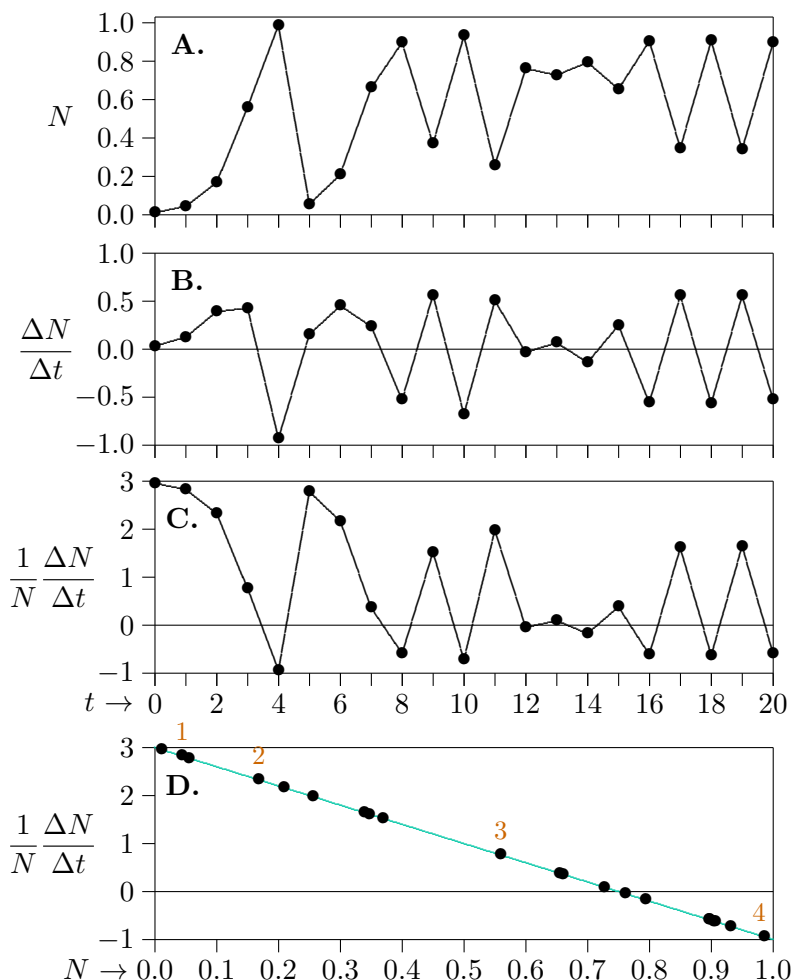


**Table 7.1.** *Hypothetical insect data.*

(A) t	(B) N	(C) DeltaN	(D) DeltaI
0	11,107	32,828	2.956
1	43,935	124,082	2.824
2	168,017	391,133	2.328
3	559,150	426,855	0.763
4	986,005	-930,810	-0.944
5	55,195	153,401	2.779
6	208,596	451,738	2.166
7	660,334	236,838	0.359
8	897,172	-528,155	-0.589
9	369,017	562,357	1.524
10	931,374	-675,708	-0.725
11	255,666	505,537	1.977
12	761,203	-34,111	-0.045
13	727,092	66,624	0.092
14	793,716	-138,792	-0.175
15	654,924	249,071	0.380
16	903,995	-556,842	-0.616
17	347,153	559,398	1.611
18	906,551	-567,685	-0.626
19	338,866	557,277	1.645
20	896,143		

data are simply generated from a difference equation, with oscillations induced by overshooting the carrying capacity and getting knocked back to different places again and again each time the population recovers.

The repeated growth and setbacks are visible in the phenomenological graph of population growth (Figure 7.2, Part A). It's easy to see here that the population grows from low levels through year 4, declines drastically in year 5, then rises again and oscillates widely in years 8 through 12. The next



**Figure 7.2.** Four graphs of chaos.  $r = 3$ ,  $s = -4$ .  $N$  is in millions.

four years show smaller oscillations, and in years 16 through 20 there are two sets of nearly identical oscillations.

The next phenomenological graph, Part B, shows not the population over time but the *change* in population over time. The difference in population size from the first year to the following year is about  $\Delta N = 33,000$  ( $44,000 - 11,000 = 33,000$ ). Similarly, the difference in time between years 1 and 2 is just  $\Delta t = 2 - 1 = 1$ . So  $\Delta N/\Delta t$  is about  $33,000/1$ , or in units of the graph, 0.033 million. Year 0 is therefore marked on the graph vertically at 0.033. Review Chapter 5 for why  $\Delta$  is used here rather than  $dN$ .

For the second year, the population grows from about 44,000 to about 168,000, so  $\Delta N/\Delta t = (168,000 - 44,000)/1 = 124,000$ , or 0.124 million. Year 1 is therefore marked on the graph vertically at 0.124. This continues for all years, with the exact results calculated in the **DeltaN** column of Table 7.1 and plotted in Part B of Figure 7.2. These data are still phenomenological, and simply show the annual changes in population levels rather than the population levels themselves.

In Part C we add a bit of biology, showing how many net offspring are produced annually *by each individual* in the population. This is  $\Delta N/\Delta t = 33,000/1$ , the number of new net offspring, divided by about 11,000 parental insects—about three net offspring per insect (more accurately, as shown in the table, 2.956). This can mean that three new insects emerge and the parent lives on, or that four emerge and the parent dies—the model abstracts such details away as functionally equivalent. All such per-insect (per capita)

growth rates are calculated in the **DeltaI** column of Table 7.1 and plotted in Part C of Figure 7.2.

Part C shows a little biological information—how the net number of offspring per insect is changing through time. Over the first four years it drops from almost 3 down to almost  $-1$ . Again, this could mean that 3 new offspring emerge and survive in year 0 and that the parent survives too, and that by year 4 almost no offspring survive and the parent dies as well. The smallest the change per insect (per capita) can ever be is  $-1$ , because that means the individual produces no offspring and dies itself—the worst possible case. And since in this case  $r = 3$ , the greatest the change can be per insect is 3—realized most closely when  $N$  is very close to 0. In the end, however, even with this touch of biology added to the graph, Part C still oscillates wildly.

The order underlying the chaos finally is revealed in Part D by retaining the biology with per capita growth on the vertical axis, but adding ecology with density  $N$  on the horizontal axis. Successive years are numbered in red above the corresponding dot. Suddenly, all points fall on a straight line!

This line reveals the underlying growth equation. Remember that the growth rate is represented as  $r + sN$ , which is a straight line. It is equivalent to the algebraic form  $y = mx + b$ , only rewritten with  $s$  in place of  $m$ ,  $N$  in place of  $x$ , and  $r$  in place of  $b$ . Remember also that it is a “first-order approximation” to the general form proposed by G. Evelyn Hutchinson,  $r + sN + s_2N^2 + s_3N^3 + \dots$ , usable when the parameters  $s_2$ ,  $s_3$ , and so on are small, so that a straight line is a good approximation. And finally, remember that in terms of human

population growth, for which we have reasonably good data, a straight line is indeed a good approximation (Figure 6.3).

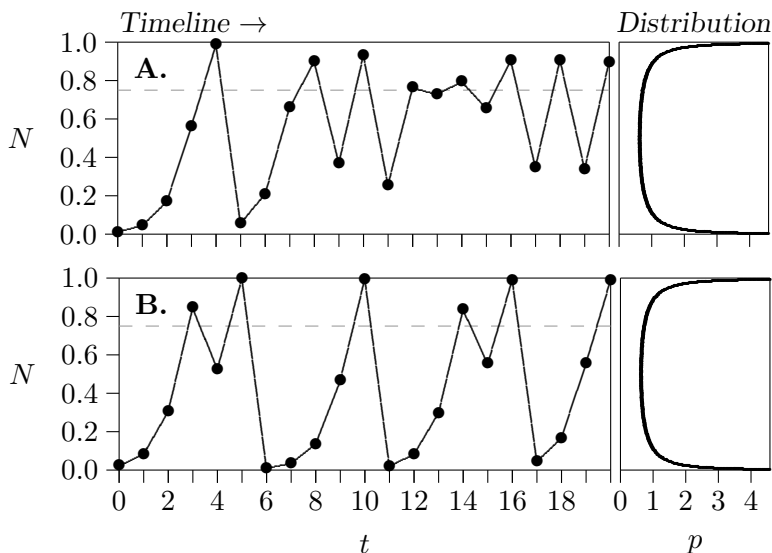
Part D of Figure 7.2 thus exposes these population dynamics as density-limited growth, because the individual growth rate on the vertical axis,  $1/N dN/dt$ , gets smaller as density on the horizontal axis,  $N$ , gets larger. And because it is a straight line, it is logistic growth. But it is different in that the finite time steps allow the population to go above its carrying capacity, forcing its growth rate negative and pulling the population back down in the next time step—whereupon the growth rate becomes positive again and is pushed up again in a confusing cascade of chaos.

## 7.3 Sensitive dependence

Below is the computer code that produced the hypothetical data for the graphs of Figure 7.2, quite similar to other code you have seen before.

```
r=3; s=-4; N=0.011107; t=0; print(N);  
while(t<=20)  
{ dN=(r+s*N)*N; N=N+dN; t=t+1; print(N); }
```

The initial condition is 11,107 insects—0.011107 million in this representation— which produces the time-pattern of Figure 7.2, Part A. But change that initial condition just a little, to 0.012107 million, and the time-pattern changes considerably. (Compare Parts A and B of Figure 7.3.) Part A is identical to Part A of Figure 7.2, but Part B of the new figure has quite a different pattern, of repeated population outbreaks—not unlike those seen in some insect populations.



**Figure 7.3.** Sensitive dependence on initial conditions. Both parts have  $r = 3$  and  $s = -(r + 1)$ , but Part A starts at 0.011107 million and Part B starts at 0.012107 million.

The emergence of very different patterns from slightly different starting points is called “sensitive dependence on initial conditions,” and is one of the characteristics of chaos.

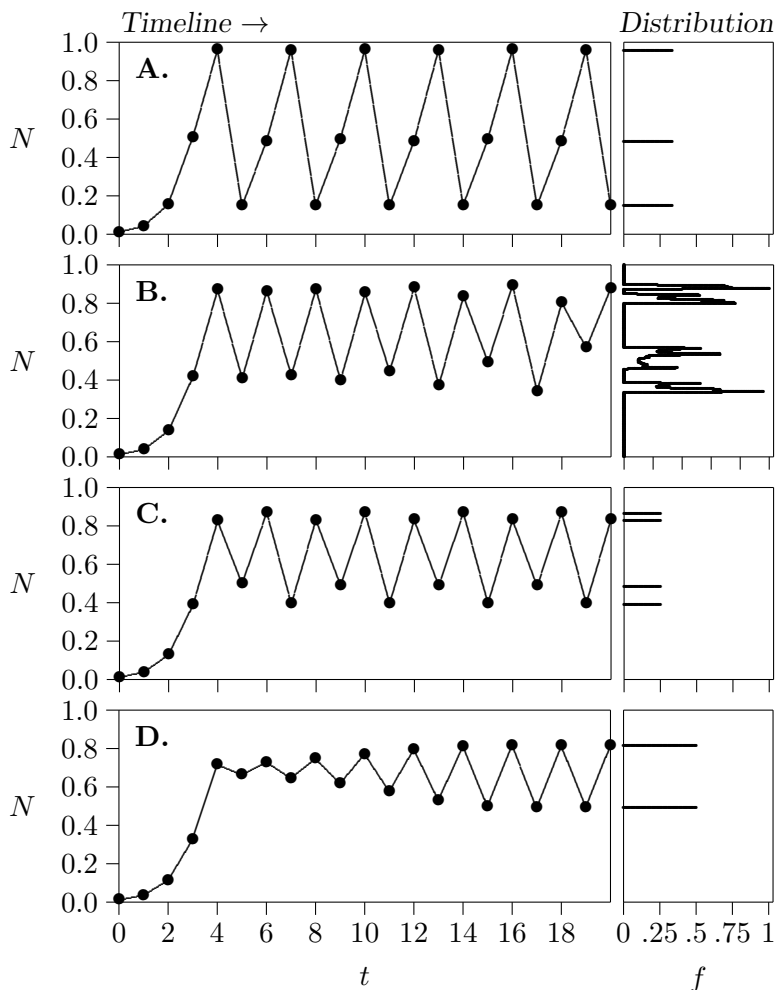
The carrying capacity in these graphs is  $K = -r/s = (-3)/(-4) = 0.75$ , representing 750,000 insects and marked with a horizontal gray dashed line. It is clear that the population is fluctuating about that equilibrium value.

Added to the right of the time line is a *distribution* of the points, showing the proportion of the time that the population occurs at the corresponding place on the vertical axis, with values to the right in the distribution representing higher proportions of time. In this case, the population spends much of the time at very low or very high values. These distributions can be determined by letting the program run for a hundred million steps, more or less, and keeping track of how many times the population occurred at specific levels. In some cases, however, as in this particular case with  $r = 3$ , the distribution can be determined algebraically. Here it is called the arcsine distribution and is equal to  $x = 1/[\pi\sqrt{y(1-y)}]$ . Though it is not particularly important to population ecology, isn't it curious to see the value  $\pi = 3.14159\dots$  emerge from a difference equation developed to understand population growth!

## 7.4 Dampening of chaos

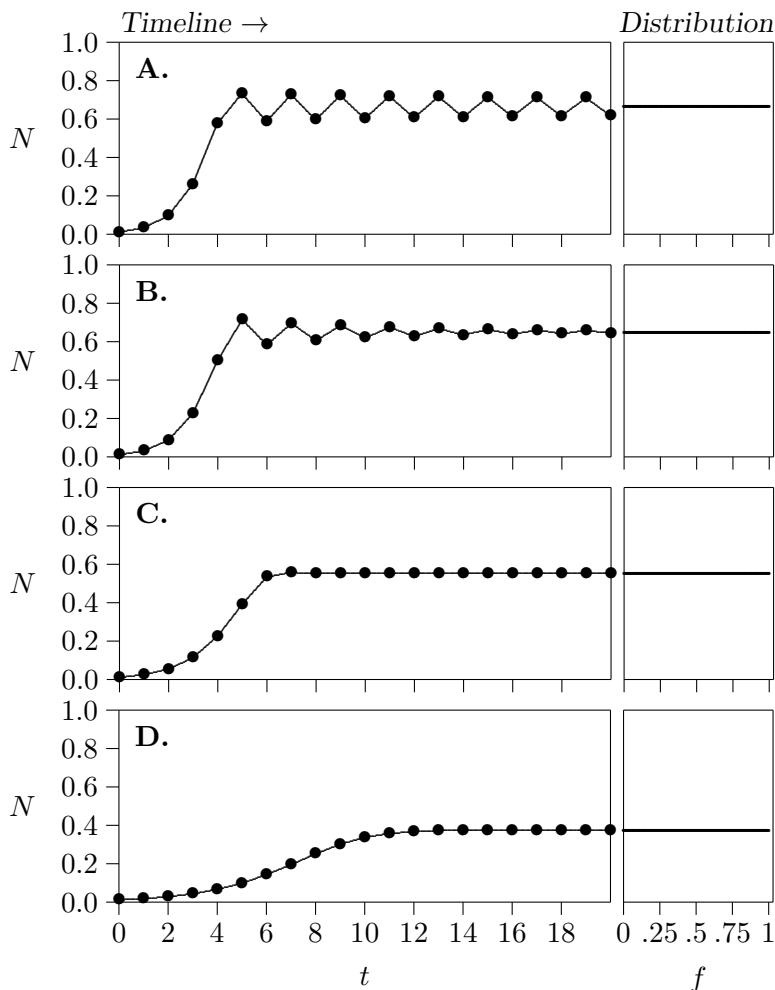
If the growth rate  $r$  diminishes, the amount that the population can overshoot its carrying capacity also diminishes, meaning that the size and severity of the fluctuations should diminish as well. Figures 7.4 and 7.5 show this happening.

When  $r$  diminishes from 3 to 2.84, for example, as in Part A of Figure 7.4, chaos vanishes and the oscillations become regular, jumping from a specific low value to a specific medium value to a specific high value, then dropping back to repeat the cycle. This is called “period three.” Sensitive dependence on initial conditions has also vanished; slight changes in the starting population will not produce different



**Figure 7.4.** Bifurcations with changing parameters. In all parts  $s = -r - 1$ . (A)  $r = 2.84$ , period 3, (B)  $r = 2.575$ , near period 4, (C)  $r = 2.48$ , period 4, (D)  $r = 2.26$ , period 2.



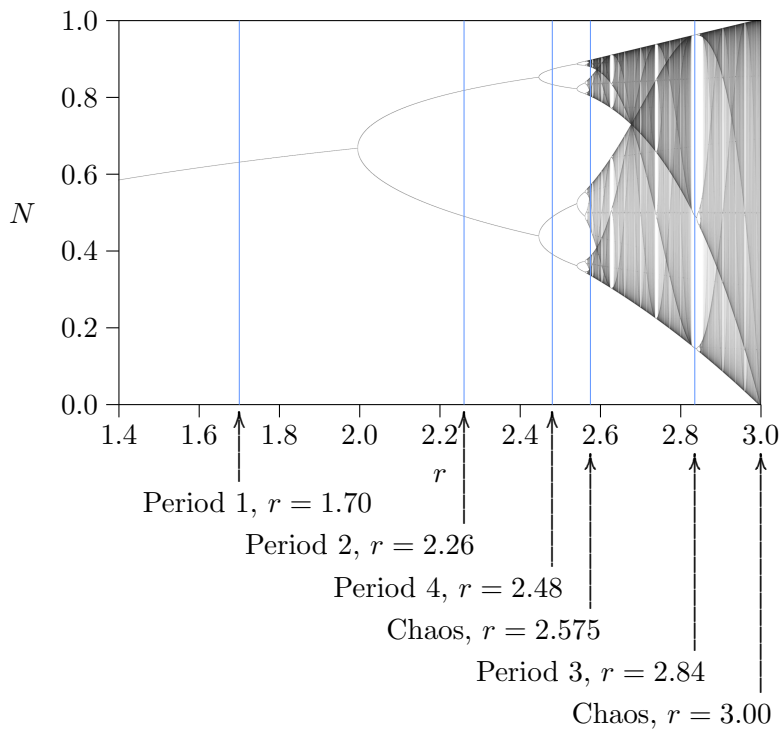


**Figure 7.5.** Changing nature of equilibrium, period 1. In all parts  $s = -r - 1$ . (A)  $r = 2.00$ , (B)  $r = 1.86$ , (C)  $r = 1.24$ , (D)  $r = 0.60$ .

patterns, as in Figure 7.3, but will end up approaching exactly the same three levels as before. The pattern is stable. Moreover, changing parameter  $r$  slightly will not change the period-three pattern to something else. The exact values of the three levels will shift slightly, but the period-three pattern will remain.

But when  $r$  is changed more than slightly—to 2.575, for example, as in Part B—the period-three pattern vanishes and, in this case, a chaos-like pattern appears. The population fluctuates among four distinct bands, with a complex distribution within each, as shown on the right in Part B. With  $r$  somewhat lower—at 2.48, for example, as in Part C—the bands coalesce into a period-four pattern, which is stable like the period-three pattern in Part A. With further reductions in  $r$ , the period-four pattern is cut in half to a period-two pattern, as in Part D, and finally to a period-one, an equilibrium pattern.

Figure 7.5 shows the progression from  $r = 3$  downward, as it changes from an oscillation toward the equilibrium, as in Parts A and B, and to a smooth approach, as in Parts C and D. This smooth approach begins when the growth rate is small enough that the population does not overshoot its carrying capacity.



**Figure 7.6.** Bifurcation diagram summarizing the discrete logistic equation.

## 7.5 Bifurcation diagram

The dynamics of all possible values of  $r$  can be summarized in a “bifurcation diagram” (Figure 7.6). In mathematical terminology, a bifurcation is a place where a tiny change in a parameter causes an extensive and discontinuous change in the behavior of the system. Figure 7.6 shows this by amalgamating the distributions on the right in Figures 7.3 through 7.5, plus distributions for all other possible values of  $r$ . Shading shows where the population spends most of its time. Starting at the right of this figure, fully in the domain of chaos, and moving to the left by reducing  $r$ , the behavior moves in and out of chaos-like patterns that never repeat and thus have no period, and also hits stable patterns of every possible period from one up toward infinity.

## 7.6 Properties

Chaos is not precisely defined in mathematics, but it occurs where:

1. Population dynamics appear to oscillate erratically, without outside influence.
2. The population has an unlimited set of different patterns of oscillation, all for the same parameter values.
3. The slightest change in the number of individuals can change the population from one pattern of oscillations to any other pattern.

It is not important that you learn all the details of chaos. The important scientific point here is that complexity can

arise from simplicity. Complex behavior of something in nature does not imply complex causes of that behavior. As you have seen, as few as two lines of computer code modelling such systems can generate extremely complex dynamics. The important biological point is that populations can oscillate chaotically on their own, with no outside influences disturbing them, and that their precise future course can be unpredictable.

Chaos and randomness in deterministic systems were discovered by mathematician Henri Poincaré★ late in the 19th century, but the knowledge scarcely escaped the domain of mathematics. In the 1960s, meteorologist Edward Lorenz★ discovered their effects in models of weather, and in the 1970s theoretical ecologist Robert May★ made further discoveries, publishing a high-profile paper that landed in scientific fields like a bombshell. The details of chaos were then worked out by a large assortment of mathematicians and scientists during the last quarter of the twentieth century. The discrete-time logistic equation examined in this chapter is now designated by Ian Stewart★ as number sixteen of seventeen equations that changed the world.

<b>Second Law of Thermodynamics</b>	$dS \geq 0$	Boltzmann, 1874
<b>Relativity</b>	$E = mc^2$	Einstein, 1905
<b>Schrodinger's Equation</b>	$ih \frac{\partial}{\partial t} \varphi = H\varphi$	Schrodinger, 1927
<b>Information Theory</b>	$H = -\sum p(x) \log p(x)$	Shannon, 1949
<b>Chaos Theory</b>	$x_{t+1} = kx_t(1 - x_t)$	May, 1975
<b>Black-Scholes Equation</b>	$\frac{1}{2} \sigma^2 S^2 \frac{\partial^2 V}{\partial S^2} + rS \frac{\partial V}{\partial S} + \frac{\partial V}{\partial t} - rV = 0$	Black & Scholes 1990

**Figure 7.7.** *The final six of seventeen equations that changed the world, as designated by Ian Steward.*

## Chapter 8

### Theory of interactions

#### 8.1 Dynamics of two interacting species

In the first part of this book you’ve seen the two main categories of single-species dynamics—logistic and orthologistic, with exponential growth being an infinitely fine dividing line between the two. And you’ve seen how population dynamics can be simple or chaotically complex.

Moving forward you will see three kinds of two-species dynamics—mutualism, competition, and predation—and exactly forty kinds of three-species dynamics, deriving from the parameters of the population equations and their various combinations.

To review, the population dynamics of a single species are summarized in the following equation.

$$\frac{1}{N} \frac{dN}{dt} = r + s N$$

Here parameter  $r$  is the “intrinsic growth rate” of the species—the net rate at which new individuals are introduced to the population when the population is vanishingly sparse, and  $s$  is a “density dependence” parameter that reflects how the size of the population affects the overall rate. Parameter  $s$  is key. If  $s$  is negative, the population grows “logistically,”

increasing to a “carrying capacity” of  $-r/s$ , or decreasing to that carrying capacity if the population starts above it. If  $s$  is positive, then the population grows “orthologically,” increasing ever faster until it encounters some unspecified limit not addressed in the equation. Exponential growth is the dividing line between these two outcomes, but this would only occur if  $s$  remained precisely equal to zero.

How should this single-species equation be extended to two species? First, instead of a number  $N$  for the population size of one species, we need an  $N$  for each species. Call these  $N_1$  for species 1 and  $N_2$  for species 2. Then, if the two species do not interact at all, the equations could be

$$\frac{1}{N_1} \frac{dN_1}{dt} = r_1 + s_{1,1} N_1$$

$$\frac{1}{N_2} \frac{dN_2}{dt} = r_2 + s_{2,2} N_2$$

Here  $r_1$  and  $r_2$  are the intrinsic growth rates for  $N_1$  and  $N_2$ , respectively, and  $s_{1,1}$  and  $s_{2,2}$  are the density dependence parameters for the two species. (The paired subscripts in the two-species equations help us address all interactions.)

$s_{i,j}$  ←———— Parameter describing density dependence  
 between two species.

↑ ↑  
 | This subscript identifies the species causing a density effect.  
 | This subscript identifies the species affected.

There are thus four possible  $s_{i,j}$  parameters here:



$s_{1,1}$ : How density of species 1 affects its own growth.

$s_{1,2}$ : How density of species 2 affects the growth of species 1.

$s_{2,1}$ : How density of species 1 affects the growth of species 2.

$s_{2,2}$ : How density of species 2 affects its own growth.

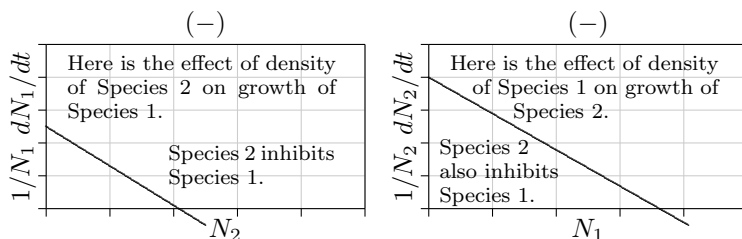
With these parameters in mind, here are the two-species equations. The new interaction terms are in blue on the right.

$$\begin{aligned}\frac{1}{N_1} \frac{dN_1}{dt} &= r_1 + s_{1,1} N_1 + s_{1,2} N_2 \\ \frac{1}{N_2} \frac{dN_2}{dt} &= r_2 + s_{2,2} N_2 + s_{2,1} N_1\end{aligned}\tag{8.1}$$

In the single-species equations, the sign of the  $s$  term separates the two main kinds of population dynamics—positive for orthologistic, negative for logistic. Similarly, in the two-species equations, the signs of the interaction parameters  $s_{1,2}$  and  $s_{2,1}$  determine the population dynamics.

Two parameters allow three main possibilities—(1) both parameters can be negative, (2) both can be positive, or (3) one can be positive and the other negative. These are the main possibilities that natural selection has to work with.

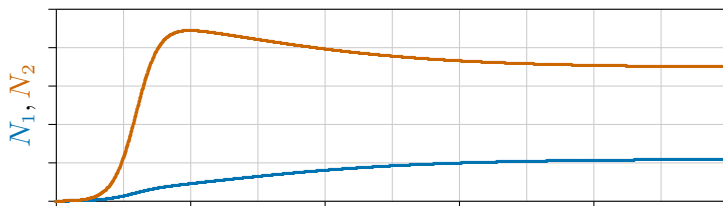
**Competition.** First consider the case where  $s_{1,2}$  and  $s_{2,1}$  are both negative, as in Figure 8.1.



**Figure 8.1.** Both interaction parameters negative, competition.

For a single species, parameter  $s$  being negative causes the population to approach a carrying capacity. The same could be expected when parameters  $s_{1,2}$  and  $s_{2,1}$  are both negative—one or both species approach a carrying capacity at which the population remains constant, or as constant as external environmental conditions allow.

One example is shown in Figure 8.2, where the population of each species is plotted on the vertical axis and time on the horizontal axis.



**Figure 8.2.** Time course of competition, one example.

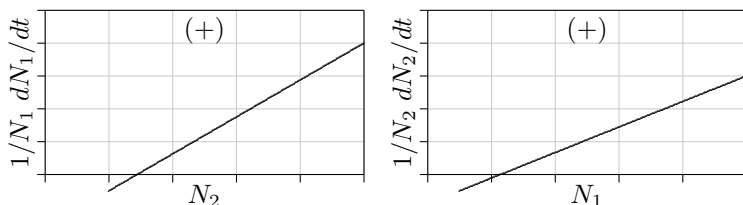
Here Species 2, in red, grows faster, gains the advantage early, and rises to a high level. Species 1, in blue, grows

more slowly but eventually rises and, because of the mutual inhibition between species in competition, drives back the population of Species 2. The two species eventually approach a joint carrying capacity.

In other cases of competition, a “superior competitor” can drive the other competitor to extinction—an outcome called “competitive exclusion.” Or, either species can drive the other to extinction, depending on which gains the advantage first. These and other cases are covered in later chapters.

In any case, when both interaction terms  $s_{1,2}$  and  $s_{2,1}$  are negative, in minus–minus interaction, each species inhibits the other’s growth, which ecologists call the “interaction competition”.

**Mutualism.** The opposite of competition is mutualism, where each species enhances rather than inhibits the growth of the other. Both  $s_{1,2}$  and  $s_{2,1}$  are positive.



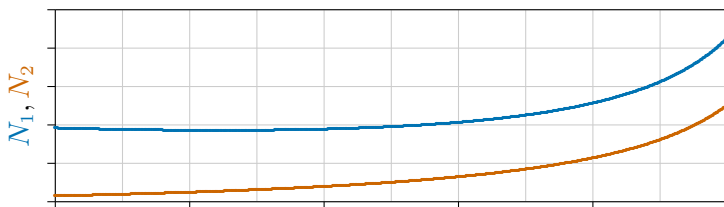
**Figure 8.3.** Both interaction parameters positive, mutualism.

Depicted in Figure 8.3 is a form of “obligate mutualism,” where both species decline to extinction if either is not present. This is analogous to a joint Allee point, where the growth curves cross the horizontal axis and become negative

below certain critical population levels. If this is not the case and the growth curves cross the vertical axis, each species can survive alone; this is called “facultative mutualism,” and we’ll learn more about it in later chapters.

For now, the important point is how mutualistic populations grow or decline over time. A single species whose density somehow enhances its own rate of growth becomes orthologistic, increasing ever more rapidly toward a singularity, before which it will grow so numerous that it will be checked by some other inevitable limit, such as space, predation, or disease.

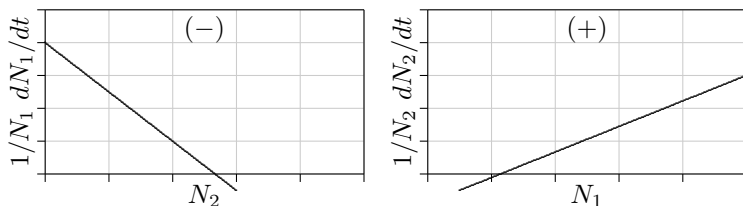
It turns out that the dynamics of two species enhancing each other’s growth are similar to those of a single species enhancing its own growth. Both move to a singularity at ever increasing rates, as illustrated earlier in Figure 4.2 and below in Figure 8.4. Of course, such growth cannot continue forever. It will eventually be checked by some force beyond the scope of the equations, just as human population growth was abruptly checked in the mid-twentieth century—so clearly visible earlier in Figure 6.3.



**Figure 8.4.** Time course of unchecked mutualism.

**Predation.** The remaining possibility for these two-species equations is when one interaction parameter  $s_{i,j}$  is positive and the other is negative. In other words, when the first species enhances the growth of the second while the second species inhibits the growth of the first. Or vice versa. This is “predation,” also manifested as parasitism, disease, and other forms.

Think about a predator and its prey. The more prey, the easier it is for predators to catch them, hence the easier it is for predators to feed their young and the greater the predator’s population growth. This is the right part of Figure 8.5. The more predators there are, however, the more prey are captured; hence the lower the growth rate of the prey, as shown on the left of the figure.  $N_1$  here, then, represents the prey, and  $N_2$  represents the predator.



**Figure 8.5.** Interaction terms of opposite signs, predation.

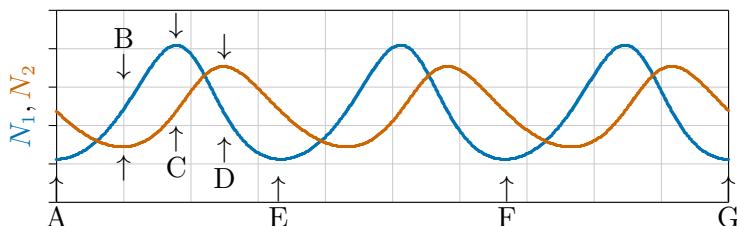
Prey can survive on their own, without predators, as reflected on the left in positive growth for  $N_1$  when  $N_2$  is 0. Predators, however, cannot survive without prey, as reflected on the right in the negative growth for  $N_2$  when  $N_1$  is 0. This is like an Allee point for predators, which will start to die out if the prey population falls below this point.

The question here is this: what will be the population dynamics of predator and prey through time? Will the populations grow logistically and level off at a steady state, as suggested by the negative parameter  $s_{1,2}$ , or increase orthologistically, as suggested by the positive parameter  $s_{2,1}$ ?

Actually, they do both. Sometimes they increase faster than exponentially, when predator populations are low and growing prey populations provide ever increasing per capita growth rates for the predator, according to the right part of Figure 8.5. In due time, however, predators become abundant and depress prey populations, in turn reducing growth of the predator populations. As shown in Figure 8.6, the populations oscillate in ongoing tensions between predator (red line) and prey (blue line).

Examine this figure in detail. At the start, labeled A, the prey population is low and predators are declining for lack of food. A steady decline in the number of predators creates better and better conditions for prey, whose populations then increase orthologistically at ever accelerating per capita rates as predators die out and conditions for prey improve accordingly.

But then the situation turns. Prey grow abundant, with the population rising above the Allee point of the predator, at B. The number of predators thus start to increase. While predator populations are low and the number of prey is increasing, conditions continually improve for predators, and their populations grows approximately orthologistically for a time.



**Figure 8.6.** Time course of predation.

Then predators become abundant and drive the growth rate of the prey negative. The situation turns again, at C. Prey start to decline and predator growth becomes approximately logistic, levelling off and starting to decline at D. By E it has come full circle and the process repeats, ad infinitum.

While Figure 8.6 illustrates the classical form for predator–prey interactions, other forms are possible. When conditions are right, the oscillations can dampen out and both predator and prey populations can reach steady states. Or the oscillations can become so wild that predators kill all the prey and then vanish themselves. This assumes some effectively-zero value for  $N_1$  and  $N_2$ , below which they “snap” to zero. Or prey populations can become so low that predators all die out, leaving the prey in peace. Or both can go extinct. Or, in the case of human predators, the prey can be domesticated and transformed into mutualists. More on all such dynamics in later chapters.

## 8.2 Code for two species

Below is computer code for two-species dynamics—a logical expansion of the code for one-species dynamics you saw earlier on pages [20](#) [36](#) [40](#) [48](#) [76](#) and elsewhere.

The code here produced the graph in [Figure 8.2](#) and, with other values for  $N_i$ ,  $r_i$ ,  $s_{i,j}$ , also produced the graphs in [Figures 8.4](#) and [8.6](#).

```
N1=.01; N2=.01;
r1=0.5; r2=0.8;
s11=-0.08; s12=-0.03; s21=-0.09; s22=-0.06;

t=0; dt=.0001; tmax=75; step=0;
print(c(t, N1, N2));

while(t<tmax)
{ dN1=(r1+s11*N1+s12*N2)*N1*dt;
  dN2=(r2+s21*N1+s22*N2)*N2*dt;

  N1=N1+dN1; if(N1<0) N1=0;
  N2=N2+dN2; if(N2<0) N2=0;

  t=t+dt; step=step+1;
  if(step==1000)
  { print(c(t, N1, N2)); step=0; }
```

This code uses a time step  $dt$  of  $1/10,000$  but displays only every 1000th time step, using the variable named **step**. This is a reliable way to display output periodically, because **step** takes on only integer values 0, 1, 2, ... Watching variable **t** for the same purpose may not be reliable; **t** has rounding errors in its fractional portion, which typically is represented only approximately by the computer.



By the way, here is a crucial requirement for coding multi-species dynamics: you must update all of the  $N_i$  together. You might be tempted to shorten the code by writing the following, getting rid of the `dN1` and `dN2` variables.

```
N1=N1+(r1+s11*N1+s12*N2)*N1*dt; if (N1<0) N1=0;
N2=N2+(r2+s21*N1+s22*N2)*N2*dt; if (N2<0) N2=0;
```

This shortened code, however, contains a serious bug that could be difficult to detect. (A “bug” is the computerese term for any mistake in computer code, typically one that goes undetected.) The calculation of `N2` on the second line uses the *new* value of `N1`, not the *present* value. This will generate subtly incorrect results that could be costly—if, for example, you were using the code to project the course of an epidemic.

Careful code reviews with experienced colleagues are one way to help avoid such bugs. If the problem is important enough, having the code written independently by two or more people not communicating with each other, except by accepting the same specifications and comparing the final results, is a way to approach correctness. This is like independent replication of scientific experiments. Other methods of ensuring that code is correct are addressed later.

### 8.3 Summary of interactions

In summary, based on the effects of each population on the other, two species can interact mainly in three different ways, as shown in Figure 8.7. Competition is a ‘ $- -$ ’ combination, mutualism is ‘ $+ +$ ’, and predation is ‘ $+ -$ ’, in either order.

		Effect on Growth Rate of Species 1	
		$-$	$+$
Effect on Growth Rate of Species 2	$-$	$- -$ competition	$- +$ predation
	$+$	$+ -$ predation	$+ +$ mutualism

**Figure 8.7.** Summary of species interactions based on signs of their interaction parameters.

Sandwiched between the boxes above are special cases where one of the interaction terms is zero, or very close to zero. These are called “commensalism,”★ when one parameter is positive and the other is zero, or “amensalism,”★ when one parameter is negative and the other is zero. We won’t focus further on these special cases.

## Chapter 9

### Embodied by natural selection

The absolute simplicity of the three plus-minus combinations for two-species dynamics, explored in the previous chapter, is converted by natural selection into physical forms of splendid complexity—unexpected and subtle, spectacular and sublime, stunning and beautiful.

From our human perspective, some details appear to embody timeless altruism and kindness, others unbounded horror and cruelty. But nature seems to implement material possibilities without regard to human values, and we are left merely to observe and wonder, and strive to understand.

At this point, to gain perspective before proceeding further, it is well to examine at least a tiny subset of ecological reality. The range of examples of multi-species interactions looks endless, and even within individual organisms are interactions among multiple species.

At the deepest level, the eukaryotic cell seems to have been created of interactions among separate prokaryotic species one or two billion years ago. Mitochondrial genomes are separate genomes within the cell with parallels to bacterial genomes, but mitochondria are no longer able to live on their own except under very special circumstances. Chloroplasts are similar. These are mutualisms at the very basis of complex life. Other mutualisms, like those with gut bacteria, form higher levels.

Mutualisms among pollinators and flowers are an ingenious arrangement for the fertilization of immobile organisms. A bee, for example, collects pollen as a food source and in the process spreads pollen from plant to plant. Plants advertise the pollen with bright flowers, and provide sweet nectar as an additional attraction (Figure 9.1, left).



**Figure 9.1.** *Pollination mutualism.*

A small mammal can act similarly, drinking nectar from one plant, getting pollen on its whiskers, and transferring the pollen when it drinks from another plant, in turn pollinating that plant (Figure 9.1, middle).

A fascinating pollination mutualism extends across the wetlands of the North American Upper Midwest, in marsh milkweed, *Asclepias incarnata* (Figure 9.1, right). Mutualisms are not necessarily perfect, and each member can be exploited in some small way. In this case, pollinators land on the milkweed flower and stand on “landing platforms” while taking nectar. But the platforms are not secure; they are curved and slightly difficult footholds. A pollinator’s legs slip into cracks between the platforms and, when the pollinator pulls its leg out, there are “saddle bags” of pollen (pollinia) wrapped around its leg, which can’t be dislodged.

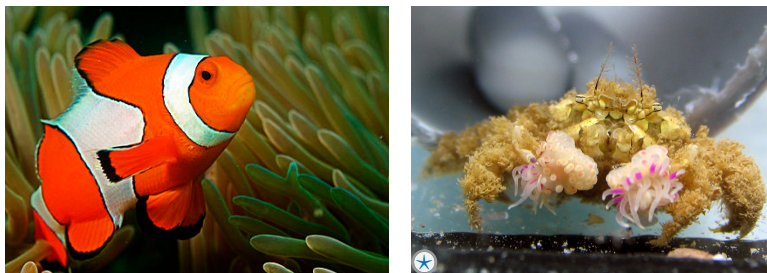
As it flies to a another flower, the saddle bags rotate forward so they easily dislodge, and they're pulled off when the pollinator slips on another insecure landing platform of the corresponding species.

In another example, warthogs (Figure 9.2 left) attract abundant ticks. What better place, then, for Oxpeckers to find morsels of food than in the bristly fur of a water buffalo? A little blood in the tick is probably a bonus. This is good for the water buffalo, good for the oxpecker, and not good for the tick. This three-species interaction is (1) predation on the water buffalo by the tick, (2) predation on the tick by the oxpecker, and thus (3) mutualism between water buffalo and oxpecker. It is an “enemy of my enemy is my friend” interaction, one of the forty kinds of three-species interactions you will see in upcoming chapters.



**Figure 9.2.** *Mutualisms through a third species.*

Likewise, ants ward off potential predators from aphids (Figure 9.2 middle), and “cleaner fish” swim freely within the mouth of a large fish (Figure 9.2 right) while they remove the fish’s parasites.



**Figure 9.3.** *Mutualism with a dangerous partner.*

Sea anemones have stinging tentacles that other fish must avoid, but clown fish can resist the sting (Figure 9.3 left). This mutualism is more complex. The clown fish protect themselves from predators by living among the anemones, and their bright colors may attract predators who become prey for the anemone. Clown fish eat scraps of food missed by the anemone, plus their own food from the water column, and provide nitrogen to the anemone from their digested waste. These are intricate mutualisms, in which specifically matched species of clown fish and anemone have become permanent partners.

Pom-pom crabs★ employ sea anemones as weapons (Figure 9.3, right), carrying two anemones and waving them in a dance to dissuade approaching predators. Crabs are sloppy eaters, so the sea anemones get the benefit of the mess as payment.



**Figure 9.4.** *Mutualism with people.*

Early on, our hunter-gatherer predecessors were predators, but later they domesticated some of their prey, changing some predator-prey interactions to mutualisms. From the point of view of domesticated sheep (Figure 9.4, left), humans may not be ideal mutualists. We protect them from wolves, harbor them from disease, and shield them from the worst vagaries of weather. But we also confine them to pens, shear off their wool, and kill and eat their lambs. Yet as agriculture advanced, the more people there were on the planet, and the more sheep there were, and vice versa. This is the ecological making of a mutualism.

It is similar with crops. Instead of gathering grain and fruit from forest and field, we cleared areas specifically for domesticated plants. We protect the crops from competition with other plants, work to keep them free of disease, and add water and nutrients to the soil to help them grow. For thousands of years we used beasts of burden to accelerate

cultivation, also in mutualisms with those beasts. Now we are entering a wholly synthetic phase, in which teams of satellite-guided tractors navigate fields with the power of a thousand horses (Figure 9.4 right).

For a thought exercise, you may want to ponder our relationship with machines. If we were mutualists with draft horses, are we now mutualists with the machines that have replaced them? As you proceed through the next chapters, consider whether our relationships with our machines meet the ecological requirements of mutualisms.



**Figure 9.5.** *Herbivory.*

Herbivory is a kind of predation in which the prey is a plant. Upon detecting herbivory, the plant may pump toxins into the leaf to dissuade the herbivore. In response, the herbivore may quickly chew out a pattern to isolate part of the leaf from the toxins and then dine in relative salubrity (Figure 9.5, left).

Multitudes of leaf cutter ants can be formidable herbivores (Figure 9.5, middle), cutting luggable-sized pieces of leaves to take back to their nests. The ants do not eat the leaves, but chew them further, feed them to fungus, and then eat the



fungus—creating an ant–fungus mutualism, with ants being predators on the trees.

At a larger scale, multitudes of bison were formidable herbivores of the prairie (Figure 9.5, right). The native tallgrass prairies were wildflower gardens, with a few dozen species of grasses but hundreds of species of flowers—said to bloom a different color each week.



**Figure 9.6.** *Beaver–aspen herbivory. Or is it mutualism?*

Beavers fell whole aspen trees (Figure 9.6, left) to make their dams and lodges (middle and right), and also for food. This sounds like herbivory. At the same time, however, they girdle and kill other species of trees that they do not use as food, clearing the way for new aspen. This is mutualism.

The photo on the right in Figure 9.6 shows a pond colonized by beaver after an absence of more than a century. Though it is midsummer, a few of the trees are defoliated—including one giant bur oak—because beaver have chewed off the cambium layer all around the trees, girdling and killing them. Judiciously followed, this practice would keep the forest in an early successional stage, a condition which favors staple aspen.

Bears catching fish and a kookaburra ambushing a frog (Figure 9.7, left and middle) are simple kinds of predation. Other ambush strategies are also common. The stonefish (right) is disguised to match its background and waves a lure to attract other fish, who are then instantly swallowed whole. Despite hundreds of millions of years of evolution, the trick still works.



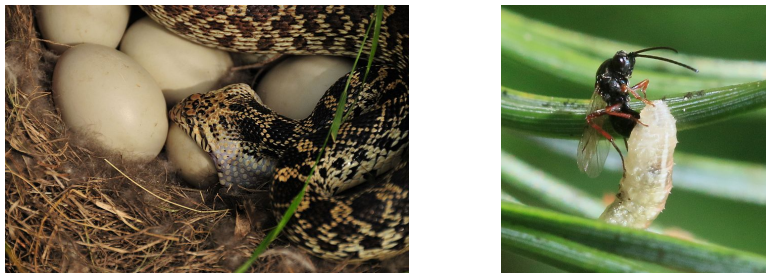
**Figure 9.7.** *Predation.*

Cats typically pursue ambush strategies, lying in wait (Figure 9.8, left), whereas dogs typically pursue sustained chasing strategies. This means that cats must be relatively odorless to avoid detection, but dogs need not be.



**Figure 9.8.** *Ambush predation.*

In a curious ambush strategy only recently achieved, herons wave gathered feathers to attract fish, then drop the feathers and grab the fish (Figure 9.8, right). Such use of feathers is apparently an animal “meme” that has spread rapidly through heron populations after being discovered by some Einstein-heron.



**Figure 9.9.** *Predation and parasitoidism.*

Species interactions can lead to remarkable evolutionary adaptations, including the non-messy way of eating an egg (Figure 9.9 left).

Nature acknowledges neither kindness nor cruelty, but parasitoidism seems one of the cruelest strategies (Figure 9.9, right). Here an *Ammophila* wasp is carrying a caterpillar not to kill and eat, but as a living hatchery for her eggs. Young wasps developing from these eggs consume the caterpillar from within as the caterpillar remains alive, transforming it into wasp larvae. Parasitoidism is widespread.



**Figure 9.10.** *Parasitism.*

When the predator is small relative to the prey, predator–prey interactions are called “parasitism.” At left in Figure 9.10 is a blood-sucking mosquito attached to an unfortunate human. At right is a beetle seemingly overwhelmed with mites. When the predator is much smaller still, it is called a “pathogen” and the interactions are called “infection” and “disease.”



**Figure 9.11.** *Plants as predators.*

Peatlands can form over vast areas where the habitat is isolated from a normal supply of nutrients (Figure 9.11, left) and life there must endure low levels of nitrogen. In this situation, some plants become predators.

The pitcher plant (Figure 9.11, middle), for example, attracts insects with nectar and then eats them to obtain nitrogen, trapping them in a pool of digestive fluid at the bottom of a tall green vase with slippery, unidirectional sides of downward-pointing hairs. The sundew (Figure 9.11, right) seems simpler, capturing unwary insects in sticky droplets and then consuming them.



**Figure 9.12.** *Predation, warnings, and deception.*

Prey develop remarkable defenses against predators, following the processes of evolution, and provide warnings of the existence of their defenses. Some such defenses and advertisements are real, like the fetid fluid sprayed by skunks (Figure 9.12 left) that can deter even large bears from attacking. The fire-bellied toad (next to left) is filled with toxins and its bright color advertises, “Do not eat me!”

Others species benefit from complex deception to keep predators away, such as the harmless clear-winged moth colored to look anything but harmless (next to right), and an edible caterpillar in disguise with a viper-like tail (right).

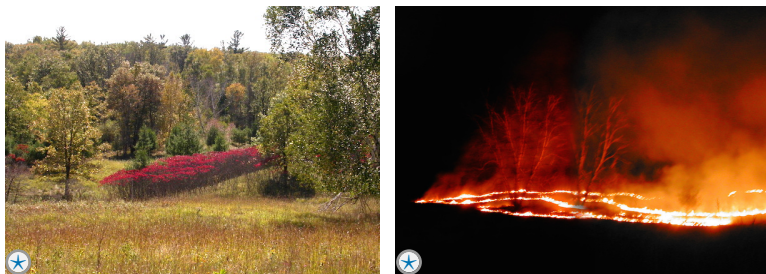


**Figure 9.13.** *Predation, camouflage, and temptation.*

Hiding is a simple, common strategy for escaping predators. On the left in Figure 9.13 is a young grasshopper on pebbles. Can you see it? Zoom in and look just a little below and to the left of center. The grasshopper's head is downward and its tail is upward and slightly to the left, with one antenna and one leg clearly visible once you see them.

The killdeer (Figure 9.13, right) tempts predators who get too close by stumbling away from the nest, feigning an injured wing and making itself look like an easy catch. Once it has lured the predator far from the nest, it lifts quite competently into the air and flies off.





**Figure 9.14.** *Competition at the North American triple ecotone.*

Examples of competition seem both more subtle and more ordinary than examples of mutualism and predation. But competition is pervasive.

North America has many ecosystems—the tundra of the Arctic, the deserts of the Southwest, the giant conifers of the Pacific Northwest—but the three largest ecosystems merge in a triple ecotone in the Upper Midwest, an area which exemplifies competition among plants. Here, the needle-leaf forests stretch north to the arctic, the broad-leaf forests extend east to the Atlantic, and the prairies' amber waves of grain flow west to the Rockies. Figure 9.14 shows a whirlpool of competition at this broad triple ecotone. White pines stand tall above the deciduous trees in the background, with Big Bluestem and other native prairie grasses setting seed in the foreground. Staghorn Sumac in red fall colors tries to hold its own in the middle, with pines invading behind it. Leaves of Bur Oak are browning for the oncoming winter.

While it may seem a peaceful scene, for the plants it is a scene of intense competition for their very existence. Fire is

a foe of trees (Figure 9.14 right), killing many instantly, and thus favoring grasses and prairie flowers. Times of moister conditions allow trees to reenter the grasslands, eventually shading the grassland vegetation to death if the moisture persists. But complexities of weather and climate have kept this competitive tension zone intact for thousands of years, with no group permanently gaining the competitive advantage.



## Chapter 10

### Phase space

In differential equation models, the basic population dynamics among species become visible at a glance in “phase space.”★  
The concepts and applications of phase spaces were origi-

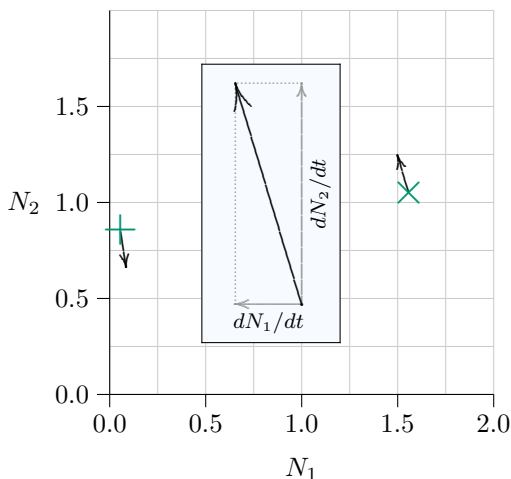


nally worked out late in the nineteenth century by Henri Poincaré and others for the dynamical systems of physics, but the mathematical foundations also apply to the theories of ecology. (At left is Poincaré seated with Marie Curie at the

initial Solvay Conference in 1911. As a point of interest, Marie Curie is the only person to have twice won the Nobel Prize for science—and she was nominated the first time before her doctoral defense!)

**I**n a phase space with two species interacting—in competition, predation, or mutualism—the abundance of one species occupies the horizontal axis and that of the other occupies the vertical axis. This makes each possible pair of population values  $(N_1, N_2)$  into a point in the phase space.

For example, a measured average abundance of 1.55 individuals per square meter for Species 1 and of 1.1 individuals per square meter for Species 2 corresponds to the point

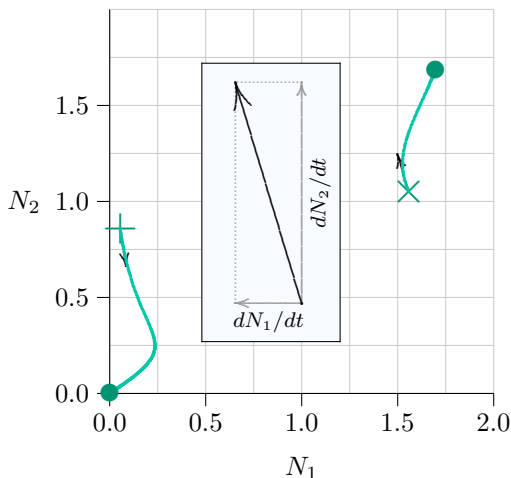


**Figure 10.1.** Phase space with two species abundances and directional derivatives also marked.

marked with an ‘ $\times$ ’ in Figure 10.1—1.55 units to the right on the horizontal axis and 1.1 units up the vertical axis. If Species 1 is rare, at 0.05 individuals per square meter, and Species 2 is at 0.85 individuals per square meter, the point is that marked with a ‘+’, near the left in Figure 10.1.

A phase space, however, is not about the size of populations, but rather about how the populations are changing over time. That change ( $dN_1/dt = f_1(N_1, N_2)$ ,  $dN_2/dt = f_2(N_1, N_2)$ ) is made visible as arrows emerging from each point.

Suppose that, at the time of the measurement of the populations marked by  $\times$ , Species 1 is decreasing slightly and Species 2 is increasing relatively strongly. Decreasing for



**Figure 10.2.** Phase space with two species abundances and trajectories to equilibria.

Species 1 means moving to the left in the phase space, while increasing for Species 2 means moving up, as shown in the inset of Figure 10.1. The net direction of change would thus be north-northwest. In the opposite direction, for the populations marked by +, if Species 1 is increasing slightly and Species 2 is decreasing relatively strongly, the direction of change would be south-southeast.

Arrows in the phase space point in the direction of immediate population change. But as the populations change, ecological conditions also change and the paths curve. Figure 10.2 shows in green how the populations change in this example as time passes. The pair of abundances starting from  $\times$  moves up, with Species 1 decreasing at first and then

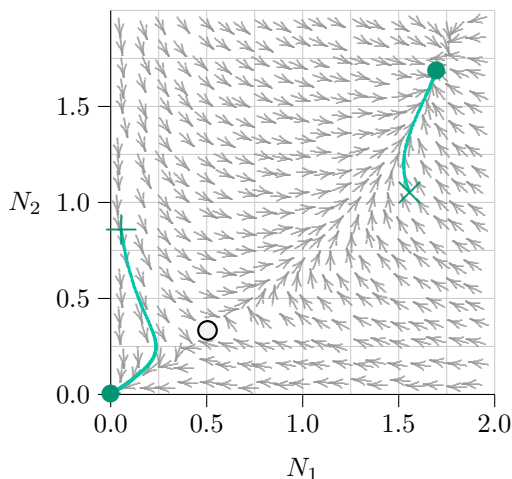
both species increasing and finally coming to rest at the green dot, which marks a joint carrying capacity.

From the  $+$ , on the other hand, Species 2 decreases uniformly but Species 1 increases at first and then reverses direction. In this case both species go extinct by arriving at the origin  $(0,0)$ . Something significant separates the  $+$  from the  $\times$ .

What separates them can be judged by calculating an arrow at many points throughout the phase space (Figure 10.3). Following the arrows from any pair of abundances  $(N_1, N_2)$  traces the future abundances that will arise as time progresses, and following the arrows backwards shows how the populations could have developed in the past. Note that the arrows seem to be avoiding the open circle near the lower left (at about 0.5, 0.3). That is an Allee point.

Some points in the phase space are exceptional: along certain special curves, the arrows aim exactly horizontally or exactly vertically. This means that one of the two populations is not changing—Species 1 is not changing along the vertical arrows, and Species 2 is unchanged along the horizontal arrows. These special curves are the *isoclines*—from the roots ‘*iso-*,’ meaning ‘same’ or ‘equal,’ and ‘*-cline*,’ meaning ‘slope’ or ‘direction.’)

The two isoclines of Species 2 are shown in red in Figure 10.4, one along the horizontal axis and the other rising and curving to the right. On the horizontal axis, the abundance of Species 2 is zero. Therefore it will always stay zero, meaning it will not change and making that entire axis an isocline. Along the other red isocline, the arrows emerging

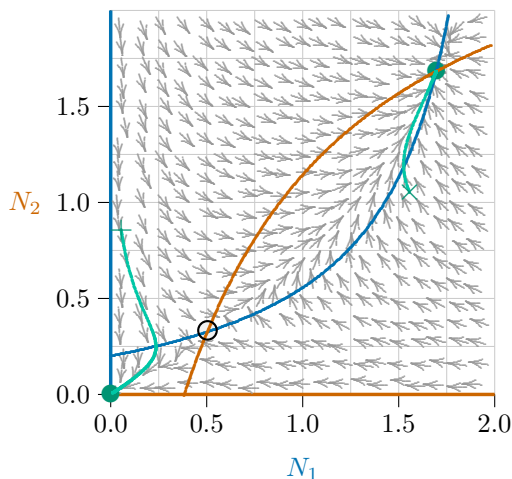


**Figure 10.3.** *Phase space with multiple equilibria.*

exactly from the isocline point exactly right or left, because the system is exactly balanced such that the abundance of Species 2 does not change—it has no vertical movement.

The situation is similar for the two isoclines of Species 1, shown in blue in Figures 10.4 and 10.5—one along the vertical axis and the other rising and curving upward. Along the blue curves, the arrows emerging exactly from the isocline point exactly up or down. Again, along the blue isocline the system is exactly balanced such that the abundance of Species 1 does not change—it has no horizontal movement.

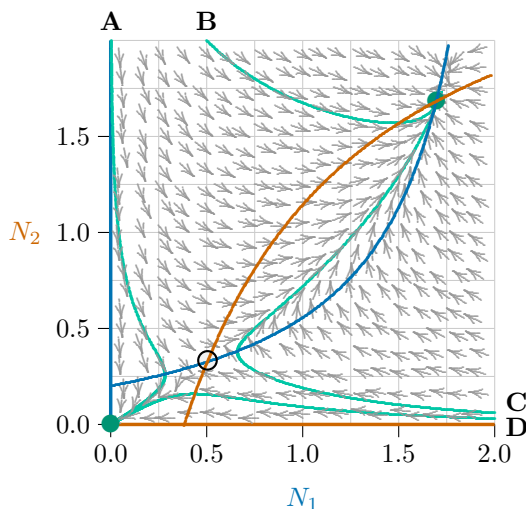
Understanding the isoclines of a system goes a long ways toward understanding the dynamics of the system. Where an isocline of one species meets an isocline of the other, the



**Figure 10.4.** Phase space with multiple equilibria and isoclines.

population of neither species changes and therefore an equilibrium forms. These are marked with circles. Notice that the arrows converge on the filled circles (stable equilibria) and judiciously avoid the open circle (unstable equilibrium). And notice that wherever a population  $(N_1, N_2)$  starts, the arrows carry it to one of two outcomes (except, technically, starting on the Allee point itself, where it would delicately remain until perturbed).

**F**or further illustration, four population growth curves are traced in green in Figure 10.5 and marked as A, B, C, and D. All start with one of the populations at 2.0 and the other at a low or moderate level. And they head to one of the two stable equilibria, avoiding the unstable equilibrium in between. You



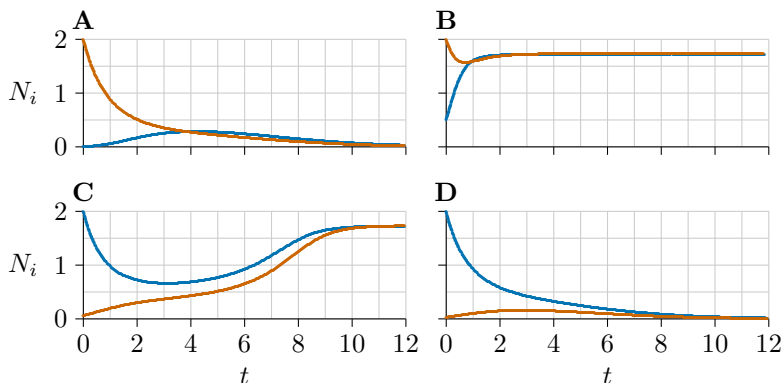
**Figure 10.5.** Phase space with multiple equilibria, isoclines, and trajectories.

can view these four growth curves plotted in the usual way, as species abundances versus time, in Figure 10.6. Blue indicates Species 1, while red indicates Species 2.

## 10.1 Surface generating the flow

A good way to understand the arrows of phase spaces is to imagine raindrops falling on a curvilinear rooftop and flowing across its surface. Figure 10.7 shows such a surface.

**W**hy should thinking of raindrops on rooftops help us understand phase spaces? It is because the differential equations themselves are situated on mathematical surfaces—albeit sometimes higher-dimensional surfaces—with points flowing



**Figure 10.6.** Trajectories from Figure 10.5 through time.

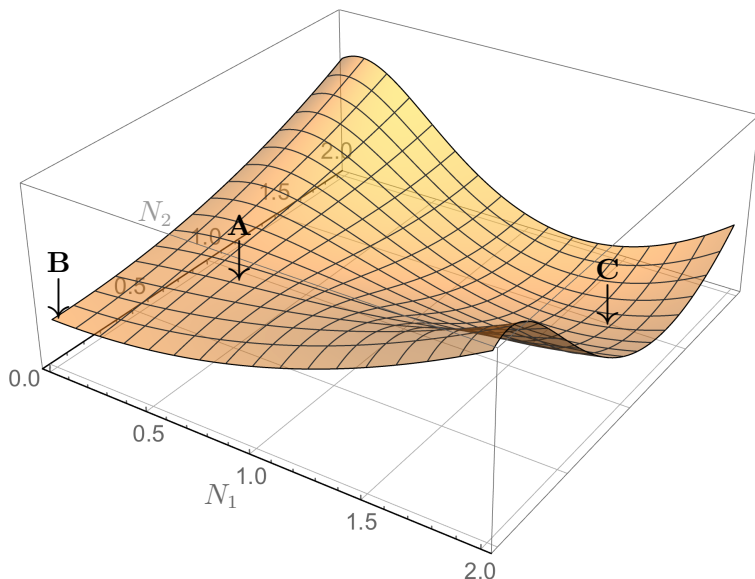
dynamically across the surfaces, just like raindrops flowing across a roof. It is not completely the same, of course, but is a useful aid to thought.

Instead of raindrops, it can also be useful to think of a marble rolling on the surface. At the bottom of the basin at Point C in Figure 10.7, a marble is trapped. The surface goes up in every direction from this point, so after any small disturbance the marble will roll to the bottom again.



Point B corresponds to the equilibrium at the origin, stable in this case, where both species are extinct. A marble resting on this surface and experiencing a small positive disturbance away from the origin must roll uphill in every direction, so it will return to that equilibrium as well. It is below the two-species Allee point.





**Figure 10.7.** Translucent surface representing the flow of Figures 10.3 to 10.5.

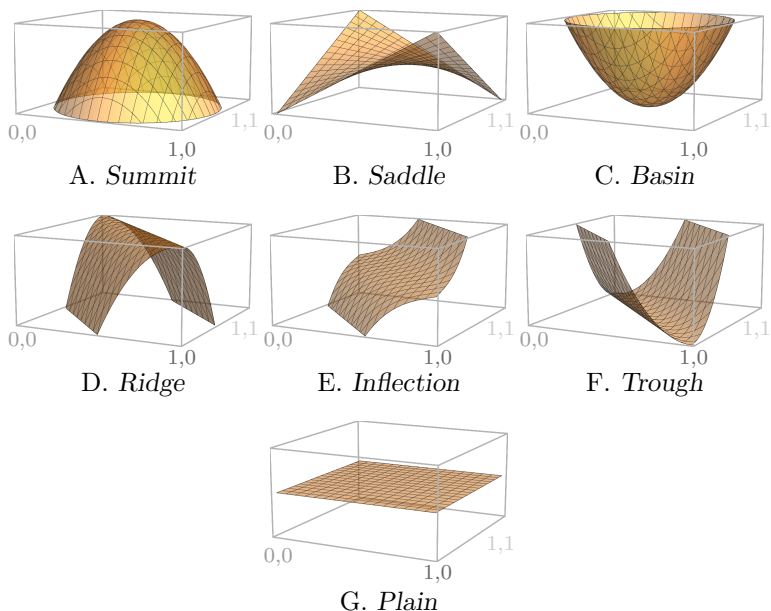
For example, Point A divides rain flowing to the left and rain flowing to the right. The basin at Point C corresponds to the carrying capacity, Point B corresponds to extinction at the origin, and Point A corresponds to the unstable Allee point.

Point A, on the other hand, corresponds to the Allee point. A marble could be balanced precariously at that place, with the slightest breath of air sending it to extinction at B

or carrying capacity in the basin at C, depending on miniscule variations in the breath. Marbles starting close to either of the axes roll to the origin, equilibrium B. Marbles starting farther from the axes are on the other side of a long ridge and roll to the carrying capacity at C.

## 10.2 Eigenvectors and eigenvalues

Think about shapes on which a marble could remain stationary, possibly balanced precariously, on a complicated two-dimensional surface in three-dimensional space, with peaks and valleys in their structure. Figure 10.8 shows seven possible configurations for remaining stationary.



**Figure 10.8.** Seven kinds of equilibria possible as part of surfaces defining two-species phase spaces.

Configuration A is a summit, a high point with respect to its surroundings. It curves downward in every direction. It is therefore unstable—a marble perched on top can roll away in any direction.

Configuration C is the opposite, a basin. The surface curves upward in every direction. It is stable because a marble resting at the bottom rolls back from a disturbance in any direction.

Configuration B is like a combination of A and C. It is called a “saddle” for its once-ubiquitous shape (right). It curves upward in some directions and downward in others. A marble resting at its very center is unstable because it can roll away in many directions.



Configurations D, E, and F are related to A, B, and C, but are level in at least one direction. A “ridge,” Configuration D, has equilibria all along its very top. A marble balanced precariously there and nudged could conceivably move to a new equilibrium along the ridge, if the nudge were aligned with infinite exactitude; almost certainly, however, the marble would roll off. This configuration has an infinite number of equilibria—all along the ridge—but none of them are stable.

A “trough,” Configuration F, is the opposite of a ridge, with equilibria all along its lowest levels. A marble resting there and nudged will move to a new equilibrium position at the base of the trough. Again there are an infinite number of equilibria—all along the base—but none are stable because,

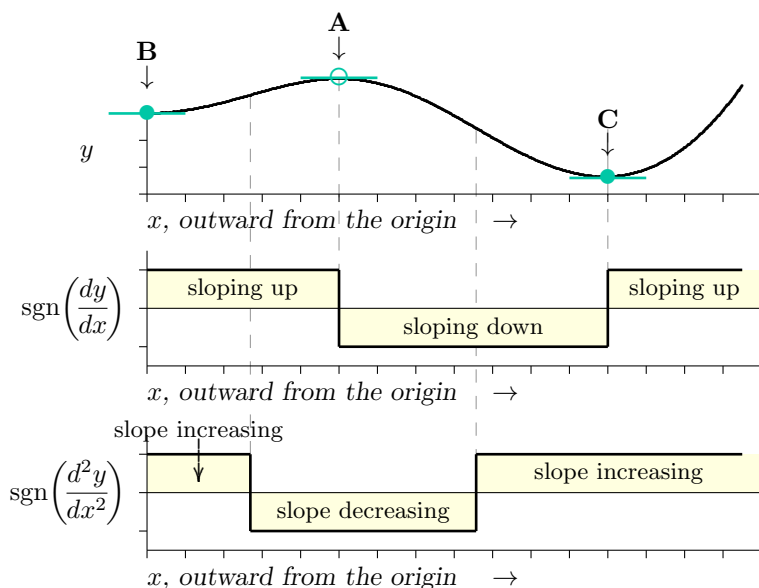
pushed along the trough, the marble does not return to its previous location. The equilibria are neutrally stable, however, in the ecological view.

An “inflection,” Configuration E, is like a combination of D and F, changing slope and becoming level, but then resuming the same direction as before and not changing to the opposite slope. It too has a level line with an infinite number of equilibria, all unstable, with marbles rolling away from the slightest nudge in half of the possible directions.

Configuration G, a perfectly flat “plain,” is perhaps easiest to understand. A marble can rest anywhere, so every point on the flat surface is an equilibrium. But a marble will not return to its former position if nudged, so no equilibrium on the flat surface is stable. In ecology this situation is sometimes called “neutrally stable;” in mathematics it is called “unstable.”

**W**ith three-dimensional images and human cognitive power, it is possible to visualize a surface at a glance, such as in Figure 10.7, and judge the implications for populations growing according to equations that correspond to that surface. You can see at a glance if it is curving up everywhere or down everywhere, if it combines upward and downward directions, or if it has level spots. You can classify each equilibrium into the configurations of Figure 10.8. But how can that judgement be quantified, made automatic?

The method of *eigenvectors* and *eigenvalues*★ accomplishes this. Think of the prefix *eigen-* as meaning “proper,” as in “proper vector” or “proper value.” The idea will become clear shortly. The method of eigenvectors and eigenvalues



**Figure 10.9.** A slice through the surface of Figure 10.7, with the slope of the surface (its first derivative,  $dy/dx$ , middle) and changes in that slope (its second derivative,  $d^2y/dx^2$ , bottom)

was developed in stages over the course of more than two centuries by some of the best mathematical minds, and now we can apply it intact to ecology.

Think of a one-dimensional slice through the surface of Figure 10.7, successively passing through points B, A, C, and beyond. It would look like the top of Figure 10.9. As before, a marble balanced precisely at A would be unstable, ready to roll either toward B or C. The equilibrium points are level points where the slope is zero, as they are on the surface

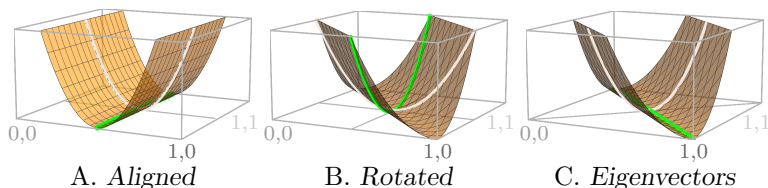
of Figure 10.7. From calculus, this is where the *derivative* is zero, where  $dy/dx = 0$ . Those slopes of zero are marked by green horizontal lines in the figure.

The middle graph of Figure 10.9 shows sign of the derivative,  $dy/dx$ , plus or minus. The sign function on the vertical axis,  $\text{sgn}(u)$ ,<sup>★</sup> is equal to zero if  $u$  is zero but is equal to plus or minus one if  $u$  is positive or negative, respectively. Whether an equilibrium is in a trough or at a summit is determined by how the slope is changing exactly at the equilibrium point. From calculus, that is the second derivative,  $d^2y/dx^2$ , recording changes in the first derivative,  $dy/dx$ —just as the first derivative records changes in the surface itself.

The sign of the second derivative is shown in the bottom part of Figure 10.9. Wherever the slope is increasing at an equilibrium point—that is, changing from sloping down on the left to sloping up on the right—that is a basin. Wherever it is decreasing at an equilibrium point—changing from sloping up at the left to sloping down at the right—that is a summit. Whether an equilibrium point is stable or not can thus be determined mathematically merely from the sign of the second derivative of surface at that point!

This is easy if there is only one species, as in the models of earlier chapters, with only one direction to consider. But it becomes tricky when two or more species are interacting, for an infinite number of directions become available.

**I**t might seem that a configuration will be a basin if the surface curves upward in both the  $x$  and  $y$  directions, as in Configuration C of Figure 10.8. But have a look at the three parts of Figure 10.10. Part A is a surface with a trough aligned with



**Figure 10.10.** *Partial derivatives, eigenvectors, and stability.*

the axes. Looking along the  $x$ -axis—which would be the  $N_1$  axis showing the abundance of Species 1—the surface is curving up on both sides of its minimum (white curve). However, looking along the  $y$ -axis—the  $N_2$  axis showing the abundance of Species 2—reveals that it is exactly level in that direction (green line), meaning the equilibrium is not stable.

But suppose the same surface is rotated 45 degrees, as in part B of the figure. The surface curves upward not only along the  $x$ -axis (white curve) but also along the  $y$ -axis (green curve). Yet the surface is the same. Contrary to what might have been expected, curving upward in both the  $x$  and  $y$  directions does *not* mean the configuration is a basin! Understanding the structure means looking in the proper directions along the surface, not simply along the axes.

This is what eigenvalues and eigenvectors do. They align with the “proper” axes for the surface, as illustrated in part C. No matter how twisted, skewed, or rescaled the surface is with respect to the axes, the eigenvectors line up with the “proper” axes of the surface, and the eigenvalues measure whether the slope is increasing or decreasing along those axes at an equilibrium. In short, if all the eigenvalues are positive,

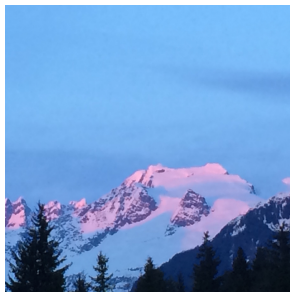


**Box 10.1.** *Rules of eigenvalues for hill-climbing systems.*

1. If all eigenvalues are negative, the equilibrium is stable.
2. If any eigenvalue is positive, the equilibrium is unstable.
3. If some or all of the eigenvalues are zero and any remaining eigenvalues are negative, there is not enough information in the eigenvalues to know whether the equilibrium is stable or not. A deeper look at the system is needed.

the equilibrium is a basin, as in Figures 10.7 C and 10.8 C. If all the eigenvalues are negative, the equilibrium is a summit, as in Figures 10.7 A and 10.8 A. And if the eigenvalues are of mixed signs, or if some are zero, then we get one of the other configurations. (See Box 10.1.)

**Climbing up versus sliding down.** All considerations thus far apply to systems that travel downhill to lower states of energy, such as raindrops flowing or marbles rolling under the influence of gravity. Dynamical systems can do the opposite—they can climb to the highest level in the locality. For example, natural selection is commonly described as climbing “fitness peaks” on abstract “adaptive landscapes.” Of course, for mathematical surfaces rather than real mountain ranges, this is just a point of view. Whether a system climbs up or



slides down depends arbitrarily on whether the mathematical surface is affixed with a plus or a minus sign in the equations.

In the bottom graph of Figure 10.9, an equilibrium in a hill-climbing system is stable if the slope is decreasing (negative sign) rather than increasing (positive sign). Because human intuition applies so well to marbles rolling off heights and settling into shallows, we have chosen to explain it intuitively that way first, but it is important to understand both ways.

It turns out that the proper axes at each equilibrium point—the eigenvectors—can be determined exactly from only four numbers, and how much the slope is increasing or decreasing at each equilibrium point—the eigenvalues—can be determined at the same time from the same four numbers. These are the four partial derivatives in what is called the “Hessian matrix”★ of the surface, or, equivalently in the “Jacobian matrix”★ of the population growth equations. An understanding of these matrices and their applications has developed in mathematics over the past two centuries.

$$\mathbf{H} = \begin{pmatrix} f_{xx} & f_{xy} \\ f_{yx} & f_{yy} \end{pmatrix}$$

By expending some effort and attention you can work the eigenvalues out mathematically with pencil and paper. However, you will likely employ computers to evaluate the eigenvalues of ecological systems. This can be done with abstract symbols in computer packages such as Mathematica or Maxima, or numerically in programming languages such as  $\mathcal{R}$ . For standard two-species systems, we have worked out all equilibria and their corresponding eigenvalues. These are

**Table 10.1.** Two-species formulae for Equation 8.1

Location	Equilibrium	Eigenvalues
Origin (Both species extinct)	$(0, 0)$	$(r_1, r_2)$
Horizontal axis (Species 1 at $K_1$ )	$\left(-\frac{r_1}{s_{1,1}}, 0\right)$	$\left(-r_1, \frac{q}{s_{1,1}}\right)$
Vertical axis (Species 2 at $K_2$ )	$\left(0, -\frac{r_2}{s_{2,2}}\right)$	$\left(-r_2, \frac{p}{s_{2,2}}\right)$
Interior (Coexistence)	$\left(\frac{p}{a}, \frac{q}{a}\right)$	$\left(\frac{-b \pm \sqrt{b^2 - 4ac}}{2a}\right)$

with

$$a = s_{1,2} s_{2,1} - s_{1,1} s_{2,2}$$

$$b = r_1 s_{2,2} (s_{2,1} - s_{1,1}) + r_2 s_{1,1} (s_{1,2} - s_{2,2})$$

$$c = -pq$$

$$p = r_1 s_{2,2} - r_2 s_{1,2}$$

$$q = r_2 s_{1,1} - r_1 s_{2,1}$$

in the ecological equations for two interacting species,

$$\frac{1}{N_1} \frac{dN_1}{dt} = r_1 + s_{1,1} N_1 + s_{1,2} N_2$$

$$\frac{1}{N_2} \frac{dN_2}{dt} = r_2 + s_{2,2} N_2 + s_{2,1} N_1$$

where

$N_1, N_2$  are population abundances of Species 1 and 2

$r_1, r_2$  are intrinsic growth rates

$s_{1,1}, s_{2,2}$  measure species effects on themselves

$s_{1,2}, s_{2,1}$  measure effects between species

```

p = r1*s22 -r2*s12;          # Compute useful sub-
q = r2*s11 -r1*s21;          # formulae.
a = s12*s21 -s11*s22;
b = r1*s22*(s21-s11)
  +r2*s11*(s12-s22);
c = -p*q;

x00=0;      y00=0;           # Compute the equilibria.
x10=-r1/s11; y10=0;          # (at the origin)
x01=0;      y01=-r2/s22;     # (on the x-axis)
x11=p/a;    y11=q/a;         # (on the y-axis)
                                # (at the interior)

v00= r1; w00=r2;             # Compute the corresponding
v10=-r1; w10=q/s11;          # four pairs of eigenvalues
v01=-r2; w01=p/s22;          # (real part only).
v11=(-b+Sqrt(b^2-4*a*c))/(2*a);
w11=(-b+Sqrt(b^2-4*a*c))/(2*a);

```

**Program 10.1.** The code equivalent to Table 10.1, for use in computer programs. `Sqrt(w)` is a specially written function that returns 0 if `w` is negative (returns the real part of the complex number  $0 + \sqrt{w}i$ ).

recorded in Table 10.1 in mathematical notation and in Program 10.1 as code, and identify the equilibria and stability for all predation, mutualism, and competition systems represented by Equation 8.1, which is copied into the table for reference.

The formulae in Table 10.1 work for any two-species RSN model—that is, any model of the form  $1/N_i \, dN_i/dt = r_i + s_{i,i}N_i + s_{i,j}N_j$  with constant coefficients—but formulae for other models must be derived separately, from a software package, or following methods for Jacobian matrices.★

**Box 10.2.** *Parameters for a sample competitive system.*

$r_1 = 1.2$	$r_2 = 0.8$	Intrinsic growth rates
$s_{1,1} = -1$	$s_{2,2} = -1$	Self-limiting terms
$s_{1,2} = -1.2$	$s_{2,1} = -0.5$	Cross-limiting terms

### 10.3 A phase space example

For an example of finding equilibria and stability, consider two competing species with intrinsic growth rates  $r_1 = 1.2$  and  $r_2 = 0.8$ . Let each species inhibit itself in such a way that  $s_{1,1} = -1$  and  $s_{2,2} = -1$ , let Species 2 inhibit Species 1 more strongly than it inhibits itself, with  $s_{1,2} = -1.2$ , and let Species 1 inhibit Species 2 less strongly than it inhibits itself, with  $s_{2,1} = -0.5$ . These conditions are summarized in Box 10.2 for reference. The question is, what are the equilibria in this particular competitive system, and what will their stability be?

First, there is an equilibrium at the origin (0,0) in these systems, where both species are extinct. This is sometimes called the “trivial equilibrium,” and it may or may not be stable. From Table 10.1, the eigenvalues of the equilibrium at the origin are  $r_1$  and  $r_2$ —in this case 1.2 and 0.8. These are both positive, so from the rules for eigenvalues in Box 10.1, the equilibrium at the origin in this case is unstable. If no individuals of either species exist in an area, none will arise. But if any individuals of either species somehow arrive in the area, or if both species arrive, the population will increase. This equilibrium is thus unstable. It is shown in the phase

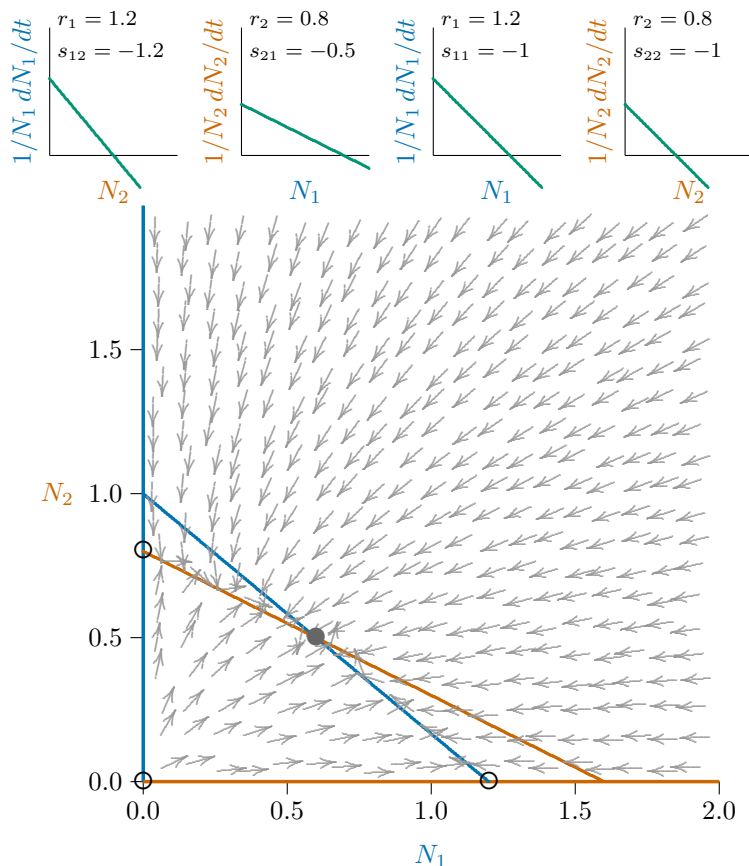
**Box 10.3.** *Calculated results for the sample competitive system.*

<i>Equilibrium</i>	<i>Coordinates</i>	<i>Eigenvalues</i>	<i>Condition</i>
Origin	(0, 0)	( 1.2, 0.8)	Unstable
Horizontal axis	(1.2, 0)	(−1.2, 0.2)	Unstable
Vertical axis	(0, 0.8)	(−0.8, 0.24)	Unstable
Interior	(0.6, 0.5)	(−0.123, −0.977)	Stable

space diagram of Figure 10.11, along with the other equilibria in the system.

On the horizontal axis, where Species 2 is not present, the equilibrium of Species 1 is  $\hat{N}_1 = -r_1/s_{1,1} = 1.2$ . That is as expected—it is just like the equilibrium of  $\hat{N} = -r/s$  for a single species—because it indeed is a single species when Species 2 is not present. As to the stability, one eigenvalue is  $-r_1$ , which is  $-1.2$ , which is negative, so it will not cause instability. For the other eigenvalue at this equilibrium, you need to calculate  $q$  from Table 10.1. You should get  $q = -0.2$ , and if you divide that by  $s_{1,1}$ , you should get 0.2. This is positive, so by the rules of eigenvalues in Box 10.1, the equilibrium on the horizontal axis is unstable. Thus, if Species 1 is at its equilibrium and an increment of Species 2 arrives, Species 2 will increase and the equilibrium will be abandoned.

Likewise, on the vertical axis, where Species 1 is not present, the equilibrium of Species 2 is  $N_2 = -r_2/s_{2,2} = 0.8$ . Calculate the eigenvalues at this equilibrium from Table 10.1 and you should get  $p = -0.24$ , and dividing by  $s_{2,2}$  give eigenvalues of  $-0.8$  and  $0.24$ . With one negative and the other



**Figure 10.11.** Phase space for the example of competition with stable coexistence summarized in Boxes 10.2 and 10.3. The arrows are calculated by code like that of Program 10.2, included for reference.

positive, by the rules of eigenvalues in Box 10.1 the equilibrium on the vertical axis is also unstable.

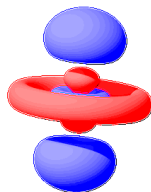
Finally, for the fourth equilibrium—the interior equilibrium where both species are present—calculate  $a$ ,  $b$ , and  $c$  from the table. You should get  $a = -0.4$ ,  $b = -0.44$ , and  $c = -0.048$ . Now the interior equilibrium is  $\hat{N}_1 = p/a = 0.6$  and  $\hat{N}_2 = q/a = 0.5$ .

But is it stable? Notice the formula for the eigenvalues of the interior equilibrium in Table 10.1, in terms of  $a$ ,  $b$ , and  $c$ . It is simply the quadratic formula!★ This is a clue that the eigenvalues are embedded in a quadratic equation,  $ax^2 + bx + c = 0$ . And if you start a project to derive the formula for eigenvalues with pencil and paper, you will see that indeed they are. In any case, working it out more simply from the formula in the table, you should get  $-0.123$  and  $-0.977$ . Both are negative, so by the rules of Box 10.1 the interior equilibrium for this set of parameters is stable.

As a final note, the presence of the square root in the formula suggests that eigenvalues can have imaginary parts, if the square root covers a negative number. The rules of eigenvalues in Box 10.1 still apply in this case, but only to the real part of the eigenvalues. Suppose, for example, that the eigenvalues are  $(-1 \pm \sqrt{-5})/2 = -0.5 \pm 1.118i$ . These would be stable because the real part,  $-0.5$ , is negative. But it turns out that because the imaginary part,  $\pm 1.118i$ , is not zero, the system would cycle around the equilibrium point, as predator–prey systems do.



In closing this part of the discussion, we should point out that eigenvectors and eigenvalues have broad applications. They reveal, for instance, electron orbitals inside atoms (right), alignment of multiple variables in statistics, vibrational modes of piano strings, and rates of the spread of disease, and are used for a bounty of other applications. Asking how eigenvalues can be used is a bit like asking how the number seven can be used. Here, however, we simply employ them to evaluate the stability of equilibria.



```

# PHASE SPACE FLOW DIAGRAM
#
# This program computes the positions and directions of the arrows
# in a phase space. It puts a few hundred arrows across the
# two-dimensional space, mostly uniformly distributed but with a
# small random variation in their starting positions. That seems
# to look better than a strictly regular arrangement.

r1= 1.0; s12=-1.0; s11=0;      # Parameters for species 1.
r2=-0.5; s21= 0.5; s22=0;      # Parameters for species 2.

xmax=3.5; ymax=2.5; grid=15;  # Size and number of grid cells.
dxy=xmax/grid;                # Spacing between grid cells.
xy0=dxy/2;                    # Indentation at left and top.
a=0.2;                        # Length of arrows.

x=y=xy0;                      # Generate points uniformly across
while(1)                      # the phase space with small random
{ N1=x+runif(1,-.03,.03);      # variations in their locations, for
  N2=y+runif(1,-.03,.03);      # best appearance in the graph.

  d1=(r1+s11*N1+s12*N2)*N1;    # Compute the magnitude of change in
  d2=(r2+s21*N1+s22*N2)*N2;    # each population from each point.

  b=sqrt(d1^2+d2^2);           # Display a vector of fixed length.
  print(c(N1, N2,
    N1+d1*a/b, N2+d2*a/b));

  x=x+dxy;                    # Advance horizontally along the row.

  if(x>xmax)                  # At the end of the row, move to the
  { x=xy0; y=y+dxy; }         # beginning of the next row.

  if(y>ymax) break; }         # Stop the loop when completed.

```

↑ Code
↑ Metacode

**Program 10.2.** Sample program in  $\mathcal{R}$  to generate a phase space of arrows, displaying the locations of the beginning and ends of the arrows, which are passed through a graphics program for display. The ‘while(1)’ statement means “while forever”, and is just an easy way to keep looping until conditions at the bottom of the loop detect the end and break out.

## Chapter 11

### State spaces

Closely related to “phase spaces”<sup>★</sup> are “state spaces.”<sup>★</sup> . While phase spaces are typically used with continuous systems, described by differential equations, state spaces are used with discrete-time systems, described by difference equations. Here the natural system is approximated by jumps from one state to the next, as described in Chapter 7, rather than by smooth transitions. While the two kinds of spaces are similar, they differ in important ways.

Inspired by the complexities of ecology, and triggered in part by Robert May’s bombshell paper<sup>★</sup> of 1976, an army of mathematicians worked during the last quarter of the twentieth century to understand these complexities, focusing on discrete-time systems and state spaces. One endlessly interesting state space is the delayed logistic equation (Aronson et al. 1982),<sup>★</sup> an outgrowth of the discrete-time logistic equation described in Chapter 7.

For a biological interpretation of the delayed logistic equation, let’s examine the example of live grassland biomass coupled with last year’s leaf litter. Biomass next year ( $N_{t+1}$ ) is positively related to biomass this year ( $N_t$ ), but negatively related to biomass from the previous year ( $N_{t-1}$ ). The more biomass in the previous year, the more litter this year and the greater the inhibitory shading of next year’s growth. The simplest approximation here is that all biomass is converted



**Figure 11.1.** *A prairie ecosystem setting seed in fall colors—Bluebird Prairie, U.S. Upper Midwest. If not burned, grazed, or mowed, grasslands can leave a thick layer of litter that inhibits the next year’s growth.*

to litter, a fixed portion of the litter decays each year, and inhibition from litter is linear. This is not perfectly realistic, but it has the essential properties for an example. Field data and models have recorded this kind of inhibition (Tilman and Wedin, Nature 1991<sup>★,★</sup>).

The basic equation has  $N_1$  as live biomass and  $N_2$  as accumulated leaf litter.  $N_1$  and  $N_2$  are thus not two different species, but two different age classes of a single species.

$$\begin{aligned} N_1(t+1) &= rN_1(t)(1 - N_2(t)) \\ N_2(t+1) &= N_1(t) + pN_2(t) \end{aligned}$$

The above is a common way to write difference equations, but subtracting  $N_i$  from each side, dividing by  $N_i$ , and making

```

r=2.27;                                # Sample growth rate.
t0=100; t1=1000;                       # Time boundaries.
r1=r-1; r2=-1; s12=-r;                 # Parameters.
N1=.4; N2=.2; t=0; dt=1;               # Initial conditions.

while(t<=t0+t1)                         # Iterate the system.
{ s21=1/N2;                             # Calculate coupling.

    dN1=N1*(r1+s12*N2)*dt;              # Advance to the next
    dN2=N2*(r2+s21*N1)*dt;              # time step.
    N1=N1+dN1; N2=N2+dN2; t=t+dt;

    if(t>t0) print(c(N1,N2)); }         # Display and repeat.

```

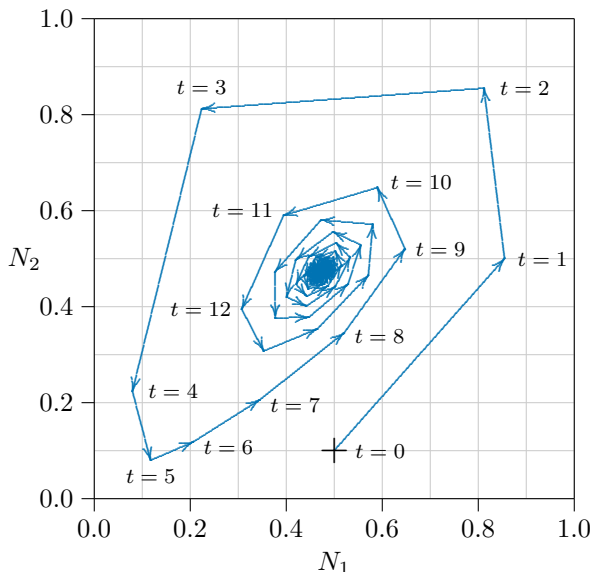
**Program 11.3.** *A program to compute successive points in the state space of the delayed logistic equation.*

$p = 0$  for simplicity gives the standard form we have been using.

$$\frac{1}{N_1} \frac{\Delta N_1}{\Delta t} = (r-1) - r N_2 = r_1 + s_{1,2} N_2$$

$$\frac{1}{N_2} \frac{\Delta N_2}{\Delta t} = -1 + \frac{1}{N_2} N_1 = r_2 + s_{2,1} N_1$$

Notice something new. One of the coefficients,  $s_{2,1}$ , is not a constant at all, but is the reciprocal of a dynamical variable. You will see this kind of thing again at the end of the predator–prey chapter, and in fact it is quite a normal result when blending functions (Chapter 18) to achieve a



**Figure 11.2.** Delayed logistic phase space with  $r = 1.9$ , spiraling inward toward an equilibrium.

general Kolomogorov form (Equation 4.3). So the delayed logistic equation is as follows:

$$\frac{1}{N_1} \frac{\Delta N_1}{\Delta t} = r_1 + s_{1,2} N_2$$

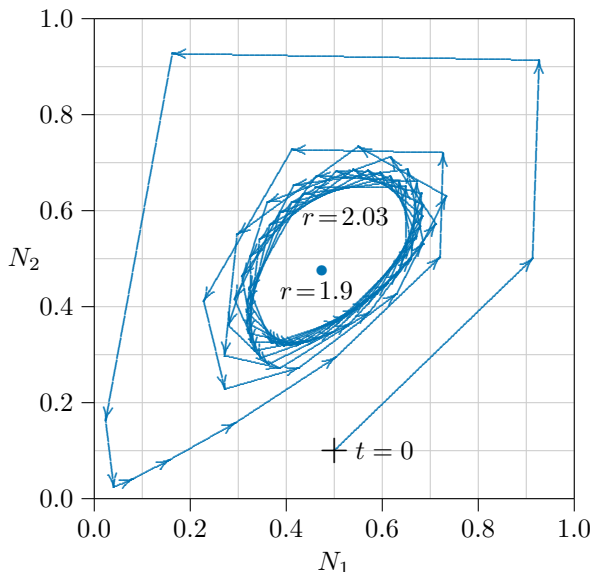
$$\frac{1}{N_2} \frac{\Delta N_2}{\Delta t} = r_2 + s_{2,1} N_1$$

where  $r_1 = r - 1$ ,  $r_2 = -1$ ,  $s_{1,2} = -r$ , and  $s_{2,1} = 1/N_1$ . Notice also that  $r_i$  with a subscript is different from  $r$  without a subscript.

For small values of  $r$ , biomass and litter head to an equilibrium, as in the spiraling path of Figure 11.2. Here the system starts at the plus sign, at time  $t = 0$ , with living biomass  $N_1 = 0.5$  and litter biomass  $N_2 = 0.1$ . The next year, at time  $t = 1$ , living biomass increases to  $N_1 = 0.85$  and litter to  $N_2 = 0.5$ . The third year,  $t = 2$ , living biomass is inhibited slightly to  $N_1 = 0.81$  and litter builds up to  $N_2 = 0.85$ . Next, under a heavy litter layer, biomass drops sharply to  $N_1 = 0.22$ , and so forth about the cycle. The equilibrium is called an “attractor”★ because populations are pulled into it.

For larger values of  $r$ , the equilibrium loses its stability and the two biomass values, new growth and old litter, permanently oscillate around the state space, as in the spiraling path of Figure 11.3. The innermost path is an attractor called a “limit cycle.”★ Populations starting outside of it spiral inward, and populations starting inside of it spiral outward—except for populations balanced precariously exactly at the unstable equilibrium point itself.

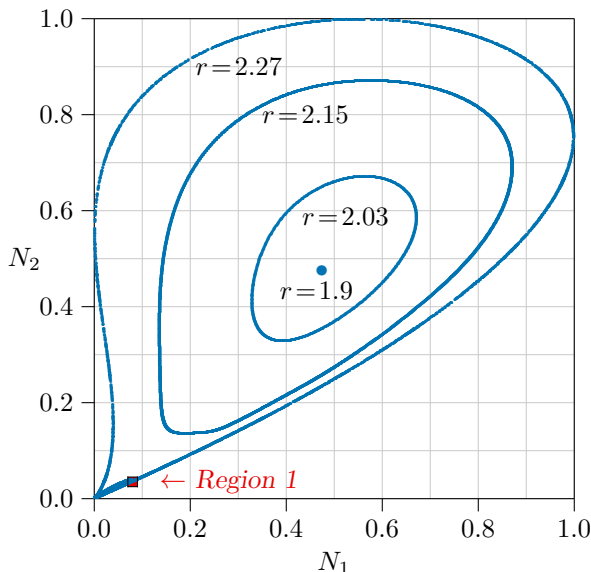
For still larger values of  $r$ , the system moves in and out of chaos in a way that itself seems chaotic. By  $r = 2.15$  in Figure 11.4, the limit cycle is becoming slightly misshapen in its lower left. By  $r = 2.27$  it has become wholly so, and something very strange has happened. A bulge has appeared between 0 and about 0.5 on the vertical axis, and that bulge has become entangled with the entire limit cycle, folded back on itself over and over again. What happens is shown by magnifying Region 1, inside the red square.



**Figure 11.3.** Delayed logistic phase space with  $r=2.03$ , spiraling toward a stable limit cycle,★ with the equilibrium point for  $r=1.9$  shown as a dot.

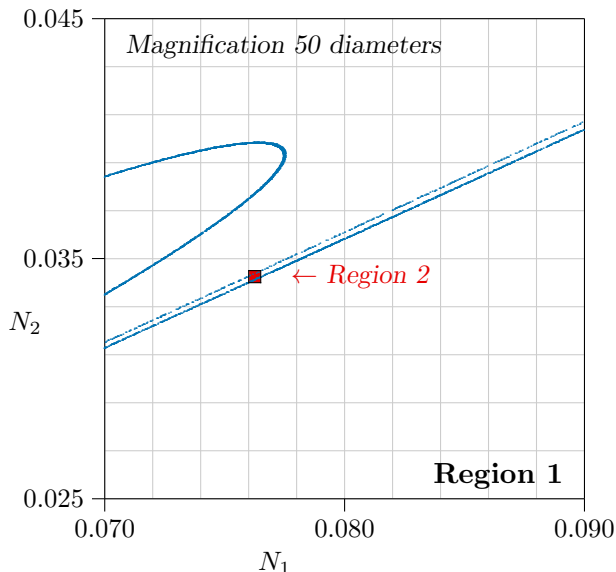
Figure 11.5 shows the red square of Figure 11.4 magnified 50 diameters. The tilted U-shaped curve is the first entanglement of the bulge, and the main part of the limit cycle is revealed to be not a curve, but two or perhaps more parallel curves. Successive images of that bulge, progressively elongated in one direction and compressed in the other, show this limit cycle to be infinitely complex. It is, in fact, not even a one-dimensional curve, but a “fractal,”★ this one being greater than one-dimensional but less than two-dimensional!★





**Figure 11.4.** Delayed logistic phase space with a stable equilibrium and three stable limit cycles for  $r = 1.9$  to  $r = 2.27$ , as marked.

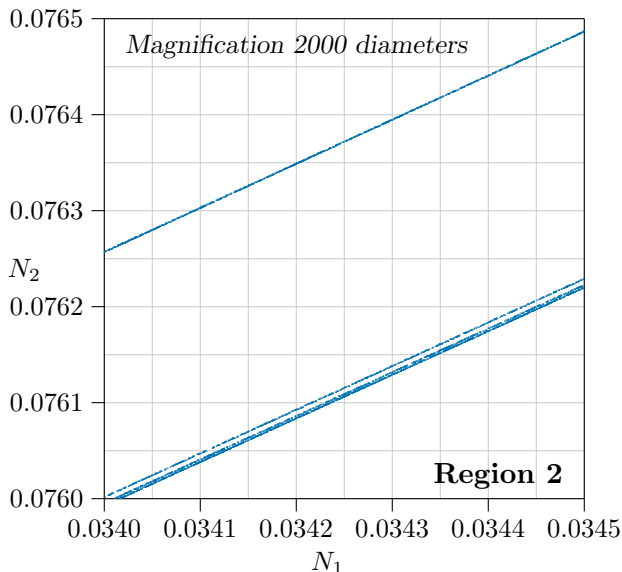
Figure 11.6. magnifies the red square of Figure 11.5, an additional 40 diameters, for a total of 2000 diameters. The upper line looks single, but the lower fatter line from Figure 11.5 is resolved into two lines, or maybe more. In fact, every one of these lines, magnified sufficiently, becomes multiple lines, revealing finer detail all the way to infinity! From place to place, pairs of lines fold together in U-shapes, forming endlessly deeper images of the original bulge. In the



**Figure 11.5.** Delayed logistic phase space with  $r = 2.27$ , Region 1 from Figure 11.4 magnified 50 diameters.

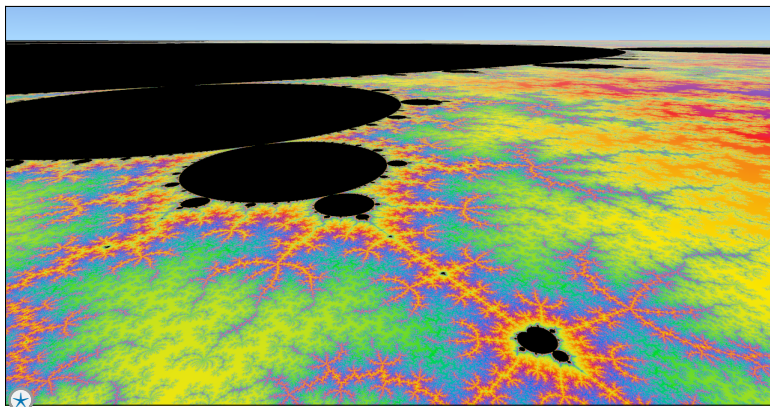
mathematical literature, this strange kind of attractor is, in fact, called a “strange attractor.”

Such strange population dynamics that occur in nature, with infinitely complex patterns, cannot arise in phase spaces of dynamical systems for one or two species flowing in continuous time, but can arise for three or more species in continuous time. And as covered in Chapter 7, they can arise for even a single species approximated in discrete time.



**Figure 11.6.** Delayed logistic phase space with  $r = 2.27$ , Region 2 from Figure 11.5 magnified an additional 40 diameters.

What we have illustrated in this chapter is perhaps the simplest ecological system with a strange attractor that can be visualized in a two-dimensional state space.



**Figure 11.7.** *Landscape of the Mandelbrot set,★ which has been called the most complex object envisioned by the human mind. It is the division between two different behaviors in a particular two-dimensional dynamical system—an infinitely complex object that is less than 2-dimensional but greater than 1.9-dimensional. We display it here for your enjoyment—for wonder and for art.*

## Chapter 12

### Predator and prey

Competition and mutualism can be understood without much attention to the sizes of the species involved. But predation is quite different. Think of a producer, the prey, and a consumer, the predator. When the consumer is extremely large and the producer very small, as with a whale and krill, the relationship is called filter feeding. There the predator kills the prey. When the producer and consumer are roughly matched in size, they are called predators and prey. When the producer is much smaller than the consumer, but still independently mobile, the relationship is called parasitism. And when the consumer is much smaller still, and has difficulty moving around on its own, the relationship is called infection and disease. Symptoms of disease are part of the ecology of disease. In parasitism and disease, the consumer often does not kill the producer.

#### 12.1 Further examples of predation

Amazing mechanisms for both capturing prey and avoiding predators have been discovered through evolution. Fulmar chicks,<sup>\*</sup> for example, can direct “projectile vomit” at predators approaching the nest too closely (Figure 12.1). This is not just icky for the predator. By damaging the waterproofing of an avian predator’s feathers, this ultimately can kill



**Figure 12.1.** *Fulmar chick with projectile vomit as predator defense.*

the predator. The chick's projectile vomit is thus a lethal weapon.

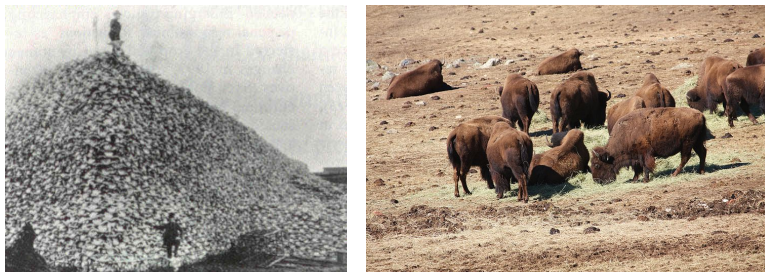
One of the most remarkable predatory weapons is that of pistol shrimp.★ These shrimp have one special claw adapted to cavitation, and are capable of shooting bullets at their prey; colonies of these shrimp are loud from the sound of these bullets. But where does an underwater crustacean get



**Figure 12.2.** *Pistol-packing shrimp shoot cavitation bullets.*

bullets? Actually, it creates them from nothing at all—from cavitation. If you’ve ever piloted a powerful motorboat and pushed the throttle too hard, or watched a pilot do so, you’ve seen the propellers start kicking out bubbles, which look like air bubbles. But the propellers are well below the water line, where there is no air. The propellers are in fact creating bubbles of vacuum—separating the water so instantly that there is nothing left in between, except perhaps very low density water vapor. Such bubbles collapse back with numerous blasts, each so powerful that it rips off pieces of bronze off the propeller itself, leaving a rough surface that is the telltale sign of cavitation.

A pistol crab snap its pistol claw together so quickly that it creates a vacuum where water used to be. With the right circulation of water around the vacuum bubble, the bubble can move, and a crab can actually project its bullet of vacuum toward its prey. When the bubble collapses, the effect is like thunder attending a lightning bolt, when air snaps together



**Figure 12.3.** *Rifle-carrying humans shoot lead bullets—bison bones and remnant herd.*

after the lightning has created a column of near-vacuum. But the consequences are quite different in water. While a loud sound might hurt the ears of a terrestrial animal, the sound does not rip apart the fabric of the animal's body. This is, however, what intense sounds in water can do, traveling through water and through the water-filled bodies of animals. In effect, pistol shrimp shoot bullets that explode near their prey and numb them into immobility. Somehow evolution discovered and perfected this amazing mechanism!


The ultimate weapons of predation, however, are those of our own species. Figure 12.3 (right) shows a remnant bison herd, a few hundred of the hundreds of millions of bison that migrated the plains not many generations ago. No matter how vast their numbers, they were no match for gunpowder and lead bullets, and they dropped to near extinction by the beginning of the twentieth century. The image at the left illustrates the epic efficiency of lead bullets by showing a



nineteenth-century pile of bison bones, with members of the predator species positioned atop and aside.

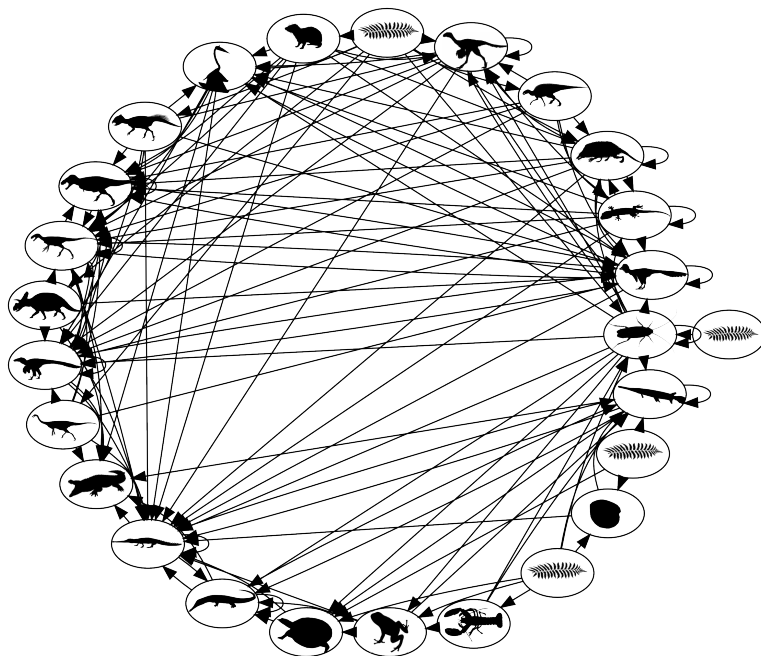
## 12.2 Ecological communities are complex

Before proceeding with simplified models of predation, we want to stress that ecological communities are complex (Figure 12.4). Fortunately, progress in understanding them comes piece by piece. Complex food webs, like the one illustrated in the figure, can be examined in simpler “motifs.”

You have seen in earlier chapters that there are two motifs for a single Species: logistic and orthologistic, with exponential growth forming a fine dividing line between them. And in the prior chapter, you saw three motifs for two species: predation, competition, and mutualism. 

Later you will see that there are exactly forty distinct three-species motifs, one of which is two prey pursued by one predator. This is called “apparent competition” because it has properties of competition.

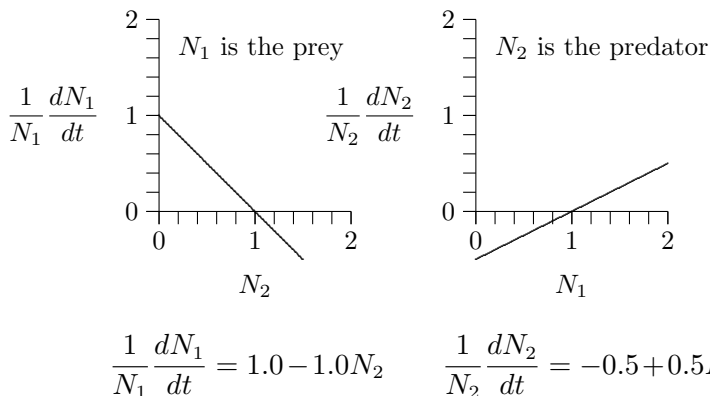




**Figure 12.4.** *Cretaceous terrestrial food web, Mitchell et al. 2012 PNAS.*

## 12.3 Predator–prey model

For the next several chapters we will consider two species, starting with one predator and one prey. Figure 12.5 depicts this situation, with one line sloping down and the other up.



**Figure 12.5.** Predator-prey interactions with corresponding equations.

The graph on the left describes the prey, because its numbers  $N_1$  are reduced when the numbers of predator,  $N_2$ , increase. Likewise, the graph on the right describes the predator, because its numbers,  $N_2$ , increase with the density of its prey,  $N_1$ . The equations of growth are revealed by the slopes and intercepts of the two lines.

Since these are both straight lines,  $y = mx + b$ , the equations can be written down simply from the geometry. The intercept on the left is +1 and the slope is  $-1$ . The intercept on the right is  $-1/2$  and its slope is  $+1/2$ . The equivalent equations of the two lines appear below the graphs.

These specific equations can be generalized using symbols in place of actual numbers, writing  $r_1$ ,  $s_{1,2}$ ,  $r_2$ , and  $s_{2,1}$  for the

intercept  $+1.0$  and slope  $-1.0$  on the left and the intercept  $-0.5$  and slope  $+0.5$  on the right, as follows.

$$\frac{1}{N_1} \frac{dN_1}{dt} = r_1 + s_{1,2}N_2 \quad \text{with } r_1 = +1.0, \quad s_{1,2} = -1.0$$

$$\frac{1}{N_2} \frac{dN_2}{dt} = r_2 + s_{2,1}N_1 \quad \text{with } r_2 = -0.5, \quad s_{2,1} = +0.5$$

Merely by writing down the form of these geometric graphs, the classic Lotka–Volterra predator–prey equations have appeared:

$$\frac{1}{N_1} \frac{dN_1}{dt} = r_1 + s_{1,2}N_2, \quad r_1 > 0, \quad s_{1,2} < 0$$

$$\frac{1}{N_2} \frac{dN_2}{dt} = r_2 + s_{2,1}N_1, \quad r_2 < 0, \quad s_{2,1} > 0$$

Here is how the equations look in many textbooks, with  $V$  for prey density and  $P$  for predator density:

$$\frac{dV}{dt} = rV - \alpha VP$$

$$\frac{dP}{dt} = \beta VP - qP$$

Volterra★ arrived at the equation rather differently than we did, with a growth rate  $r$  for the prey, reduced by a rate  $\alpha$  for each encounter between predator and prey,  $V \cdot P$ , and with a natural death rate  $q$  for predators and compensatory

growth rate  $\beta$  for each encounter,  $V \cdot P$ , between predator and prey.

To see the equivalence, divide the first equation through by  $V$  and the second by  $P$ , then set  $V = N_1$ ,  $P = N_2$ ,  $r = r_1$ ,  $q = -r_2$ ,  $\alpha = -s_{1,2}$ ,  $\beta = s_{2,1}$ . The Lotka-Volterra formulation will be revealed to be just the  $r + sN$  equations in disguise.

Figure 12.5 exposes the basic predator-prey equations from geometry, which reveal the unity of the equations of ecology, as you saw on Page 55. That analysis revealed a form of one-dimensional equation not considered in ecological textbooks—the orthologistic equation—and which is needed for understanding human and other rapidly growing populations.

Now analyze these equations a bit. Suppose predator and prey densities are both 1, say 1 individual per hectare ( $N_1 = N_2 = 1$ ). Substitute 1 for both  $N_1$  and  $N_2$ . What are the growth rates?

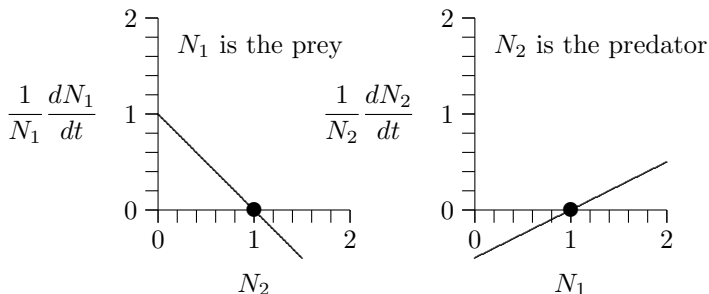
$$\frac{1}{1} \frac{dN_1}{dt} = 1.0 - 1.0 \times 1 = 0$$

$$\frac{1}{1} \frac{dN_2}{dt} = -0.5 + 0.5 \times 1 = 0$$

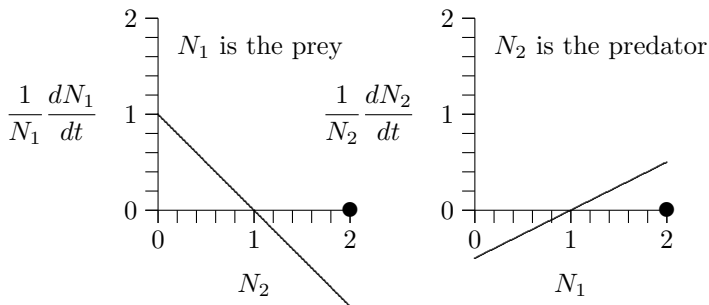
The population growth is zero for both species, so the populations do not change. This is an equilibrium.

This can be seen in the graphs below. The fact that both growth rates,  $1/N_1 dN_1/dt$  and  $1/N_2 dN_2/dt$ , cross the horizontal axis at  $N_1 = N_2 = 1$  (position of the dots) means

that growth stops for both. This is called an equilibrium, a steady state, or, sometimes, a fixed point.

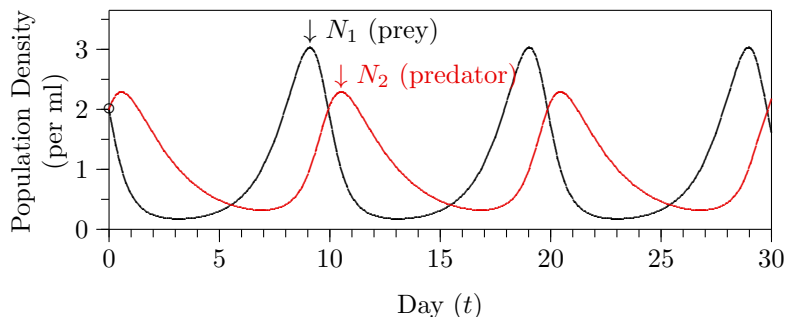


But what will happen if both populations are 2, say 2 individuals per hectare?



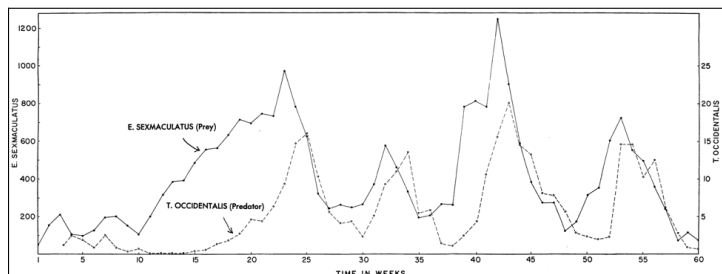
The prey growth rate,  $1/N_1 dN_1/dt$ , is negative at  $N_2 = 2$  (the line is below the horizontal axis) and the predator growth rate,  $1/N_2 dN_2/dt$ , is positive at  $N_1 = 2$  (the line is above the horizontal axis). So the prey population will decrease and the predator population will increase. Exactly how the populations will develop over time can be worked

out by putting these parameters into the program on Page 95 . Here it what it shows.



**Figure 12.6.** Dynamics of the predator–prey system of Figure 12.5 as calculated by Program 95.

For comparison, here is what early experimenters such as Gause and Huffaker showed for populations of protozoa, mites, and other small systems in the middle of the twentieth century:

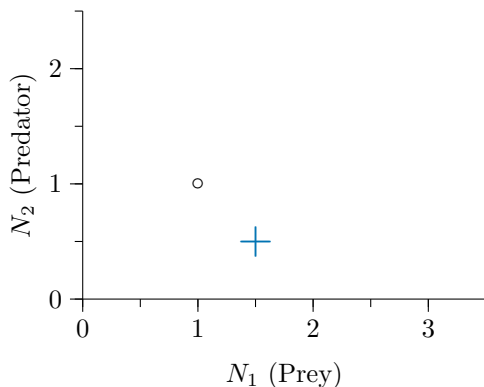


**Figure 12.7.** Dynamics in an experimental predator–prey system conducted by C. B. Huffaker★ in the 1950s with two species of mite.

The dynamics here are much the same as those shown in the calculated version of Figure 12.6 and the experimental version of Figure 12.7, but with stochasticity overlayed on the experimental system. Experimenters, however, had difficulty achieving continual cycling. In simple conditions, the predators would find the prey and eat every last one, and then the predators themselves would all die. Continual cycling could be achieved by providing the prey with places to escape, or making it difficult for the predators to move around the environment.

## 12.4 Phase space

The cycling can be understood better in phase space, where the densities of the two species are represented as two-dimensional points.





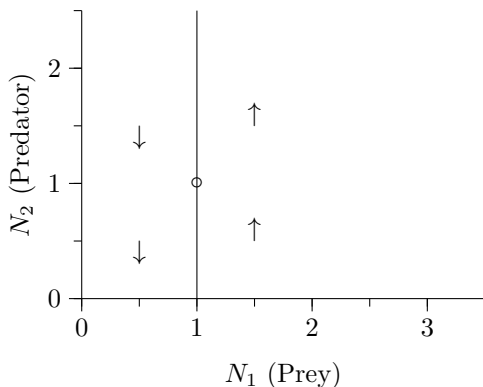
**Figure 12.8.** *Predator–prey phase space. The circle marks an equilibrium where growth of both predator and prey stops. The plus sign marks a population value of  $N_1 = 1.5$ ,  $N_2 = 0.5$ .*

For example, as explained in Chapter 10, if the prey population is 1.5 and the predator population is 0.5, the population will be 1.5 units to the right on the horizontal axis and 0.5 units up on the vertical axis, at the location of the blue plus sign in the graph.

Where does the predator population cease to grow? In the equation

$$\frac{1}{N_2} \frac{dN_2}{dt} = r_2 + s_{2,1}N_1$$

it ceases to grow where  $0 = r_2 + s_{2,1}N_1$ , or  $N_1 = -r_2/s_{2,1}$ . With  $r_2 = -0.5$  and  $s_{2,1} = 0.5$ , this is a vertical line—the predator isocline—at  $N_1 = 1$ , as in Figure 12.9.



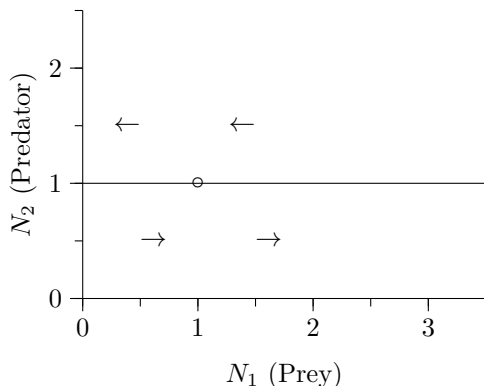
**Figure 12.9.** *The predator isocline, at which the predator population ceases to grow.*

To the left of the isocline, prey are sparse and predators decline, as indicated by the downward arrows. To the right of the isocline, in contrast, prey are abundant and predators can increase, as indicated by the upward arrows.

Likewise, where does the prey population cease to grow? In the equation

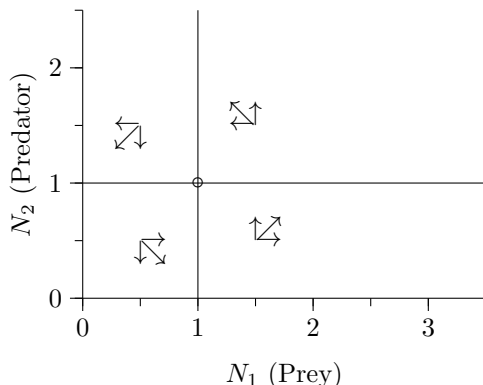
$$\frac{1}{N_1} \frac{dN_1}{dt} = r_1 + s_{1,2}N_2$$

it ceases to grow where  $0 = r_1 + s_{1,2}N_2$ , which means  $N_2 = -r_1/s_{1,2}$ . With  $r_1 = 1$  and  $s_{1,2} = -1$ , this is a horizontal line—the prey isocline—at  $N_2 = 1$ .



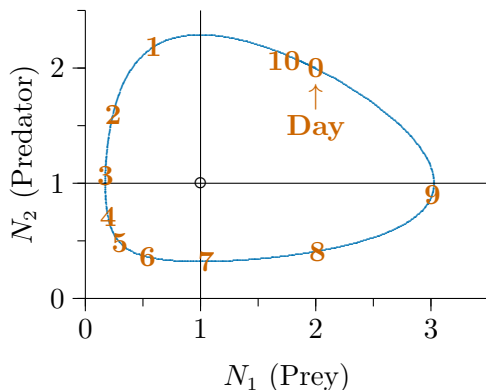
**Figure 12.10.** *The prey isocline, at which the prey population ceases to grow.*

Below the isocline, predators are sparse so prey can increase, as indicated by the arrows pointing right. Above the isocline, in contrast, predators are abundant and prey decrease, as indicated by the arrows pointing left. Putting Figures 12.9 and 12.10 together gives Figure 12.11, which shows rotation in the combined arrows.



**Figure 12.11.** Both isoclines, with both sets of arrows combined, showing the cycling.

Here the rotation can be deduced by thinking about the dynamics of predator and prey. The rotation is corroborated by using Table 10.1 to calculate the eigenvalues. The eigenvalues of the interior equilibrium turn out to be  $0 \pm 0.707i$ , a number with both real and imaginary parts. The existence of an imaginary part,  $\pm 0.707i$ , implies cycling. The real part, 0, means that eigenvalues alone cannot determine the stability—it could be stable, unstable, or neutral. In fact,

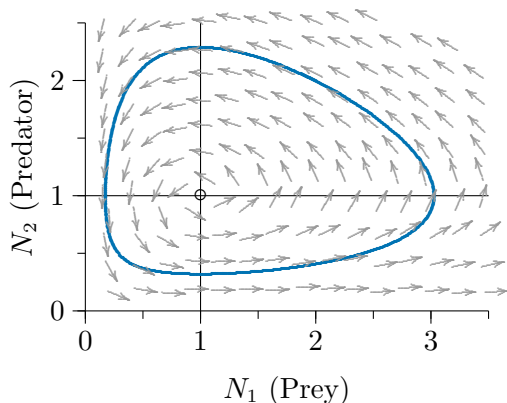


**Figure 12.12.** Days 1 through 10 marked on the cycle of Figure 12.6.

for this particular case with no self-limitation, deeper mathematical examination shows that the stability is neutral. The dynamics will rotate indefinitely, maintaining whatever cycle it started on.

Taking all the data from Figure 12.6 and plotting  $N_1$  versus  $N_2$  gives Figure 12.12. The process starts at day 0 with  $N_1 = N_2 = 2$ . One day later, prey have dropped to  $N_1 \approx 0.5$  and predators have increased to  $N_2 \approx 2.2$ , marked by the red numeral 1 on the cycle. (By the symbol ‘ $\approx$ ’, we mean “approximately equal to.”) Two days later, prey have dropped to  $N_1 \approx 0.2$  and predators have dropped to  $N_2 \approx 1.0$ , marked by the numeral 3. With predators at relatively low levels, prey then start to increase and, four days later, have reached  $N_1 \approx 1.0$ , while predators have dropped

further to  $N_2 \approx 0.3$ , marked by the numeral 7. Two days later, prey have increased to  $N_1 \approx 3.0$  and predators have increased to  $N_2 \approx 1.0$ , marked by the numeral 9. Finally, one day later the cycle begins to repeat, as marked with the numeral 10. This is another way of showing the cycling of Figure 12.6.



**Figure 12.13.** *The flow across the phase space.*

In Figure 12.13—a flow diagram, the entire phase space can be filled with arrows to show how cycling proceeds everywhere. The path of Figure 12.6, displayed in Figure 12.12, is overlaid in blue.

## 12.5 Assumptions of the basic model

This basic model of interacting predators and prey reveals the tension between population growth and decline, and shows the kind of cycling that characterizes predator–prey systems. It has, however, a number of simplifying assumptions that can be relaxed in more detailed studies, including the following:

1. The predator lives only on this prey, and perishes without it.
2. The prey has no carrying capacity of its own—only that imposed by the predator.
3. The environment is homogeneous and prey have no hiding places.
4. Growth is continuous, with no age structure, maturation periods, and so forth.
5. The number of prey taken is proportional to the number of prey present. In other words, predators are never satiated.
6. Genetics are uniform within each species, and there is no evolution.

Relaxing all of these assumptions is a book in itself, but we will relax some of them in sections ahead.



**Figure 12.14.** *Predators satiated versus sick and starving.*

## 12.6 Independent carrying capacities

Self-limitation or self-enhancement of population growth are within the  $r + sN$  framework. Below these terms are in red.

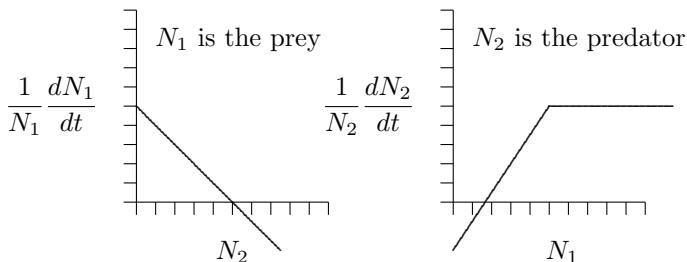
$$\begin{aligned}\frac{1}{N_1} \frac{dN_1}{dt} &= r_1 + s_{1,2}N_2 + s_{1,1}N_1 \\ \frac{1}{N_2} \frac{dN_2}{dt} &= r_2 + s_{2,1}N_1 + s_{2,2}N_2\end{aligned}$$

The self-feedback term for the prey,  $s_{1,1}$ , is typically negative, reflecting a carrying capacity for the prey in the absence of predators,  $K_1 = -r_1/s_{1,1}$ . This tends to stabilize the system, dampening oscillations and leading to a joint equilibrium of predator and prey.

On the other hand, the self-feedback term for the predator,  $s_{2,2}$ , is typically zero, meaning the predators vanish in the absence of prey. But it could be positive, indicating benefits from group hunting and the like. A positive value for  $s_{2,2}$  tends to destabilize the system, leading to enlarging oscillations.

## 12.7 Predator satiation and starvation

In the original Lotka–Volterra formulation, doubling the number of prey in the environment doubles the number of prey taken. The same is true in the equivalent  $r + sN$  formulation explored above. While this may be reasonable at low prey densities, eventually the predators become satiated and stop hunting, as in the image at left in Figure 12.14. Satiation will therefore truncate the predator growth curve at some maximum rate, as at right in Figure 12.15.

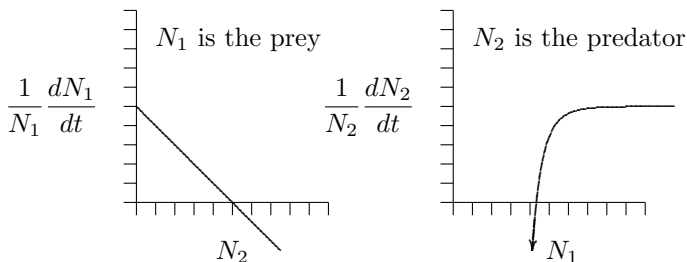


**Figure 12.15.** Predator growth truncated at a maximum number of prey taken per predator per unit of time.

In the opposite direction, if prey are not available, the predator population starves, as in the sad image at right in Figure 12.14. As indicated by a negative vertical intercept in Figures 12.5 and elsewhere, the population does not reach a maximum rate of decline. In the complete absence of prey, vertebrate predators decline more and more rapidly, reaching extinction at a definite time in the future, as induced by the increasingly large rates of decline shown in the right part of



Figure 12.16. This is a different kind of singularity that can actually occur in a finite time.



**Figure 12.16.** Vertebrate predators with asymptotic rates of consumption.

As an exercise and illustration, let us create a predator–prey system in which the predators become satiated and reach a maximum growth rate, but for which there is no maximum death rate in the absence of prey, and see where it leads.

For predators, we want to mimic the shape at right in Figure 12.16. This has the shape of a hyperbola,  $y = 1/x$ , but reflected about the horizontal axis and shifted upwards. The equation would be  $y = a - b/x$ , where  $a$  and  $b$  are positive constants. When  $x$  approaches infinity, the term  $b/x$  goes to zero and  $y$  therefore approaches  $a$ . It crosses the horizontal axis where  $x = b/a$ , then heads downward toward minus infinity as  $x$  declines to zero. Such a curve has the right general properties.

The predator equation can therefore be the following, with  $r_1$  for  $a$ ,  $s_{1,2}$  for  $-b$ , and  $N_1$  for  $x$ .

$$\frac{1}{N_2} \frac{dN_2}{dt} = r_2 + s_{2,1} \frac{1}{N_1}$$

When there are ample prey  $N_1$  will be large, so the term  $s_{2,1}/N_1$  will be small and the predator growth rate will be near  $r_2$ . As prey decline, the term  $s_{2,1}/N_1$  will grow larger and larger without limit and, since  $s_{2,1}$  is less than zero, the predator growth rate will get more and more negative, also without limit.

What about the prey equation? The important point here is that predators become satiated, so the chance of an individual prey being caught goes down as the number of prey in the environment goes up. So instead of a term like  $s_{1,2} N_2$  for the chance that an individual prey will be taken, it would be more like  $s_{1,2} N_2/N_1$ .

$$\frac{1}{N_1} \frac{dN_1}{dt} = r_1 + s_{1,2} \frac{N_2}{N_1} + s_{1,1} N_1$$

In other words, the rate of prey being taken increases with the number of predators in the environment, but is diluted as there are more and more prey and predators become satiated. Eventually, with an extremely large number of prey in the area relative to the number of predators, the effect of predators on each individual prey becomes negligible. This creates the following predator-prey system, which takes satiation and starvation into account:

$$\begin{aligned}\frac{1}{N_1} \frac{dN_1}{dt} &= r_1 + s_{1,2} \frac{N_2}{N_1} + s_{1,1} N_1 \\ \frac{1}{N_2} \frac{dN_2}{dt} &= r_2 + s_{2,1} \frac{1}{N_1}\end{aligned}$$

This system could be criticized because it is not “mass balanced.” In other words, one unit of mass of prey does not turn directly into a specific amount of mass of predators. But this is not a simple molecular system, and it at least fits more closely the realities of predator and prey behavior.

In any case, keep in mind that  $s_{1,1}$  is less than 0, to reflect limitation of prey due to crowding and other effects;  $s_{2,2}$  is equal to 0, assuming the predator is limited only by the abundance of prey;  $s_{1,2}$  is less than 0 because the abundance of predators decreases the growth of prey; and  $s_{2,1}$  is also less than 0 because as the number of prey decreases there is an increasingly negative effect on the growth of the predator.

The next step is to examine the isoclines for this new set of equations, making a phase-space graph with  $N_1$  on the horizontal axis versus  $N_2$  on the vertical. Where does the prey growth,  $1/N_1 dN_1/dt$ , cease? Working through some algebra, it is as follows:

$$\begin{aligned}\frac{1}{N_1} \frac{dN_1}{dt} = 0 &= r_1 - s_{1,2} \frac{N_2}{N_1} - s_{1,1} N_1 \\ \Rightarrow s_{1,2} \frac{N_2}{N_1} &= r_1 - s_{1,1} N_1 \\ \Rightarrow N_2 &= \frac{r_1}{s_{1,2}} N_1 - \frac{s_{1,1}}{s_{1,2}} N_1^2\end{aligned}$$

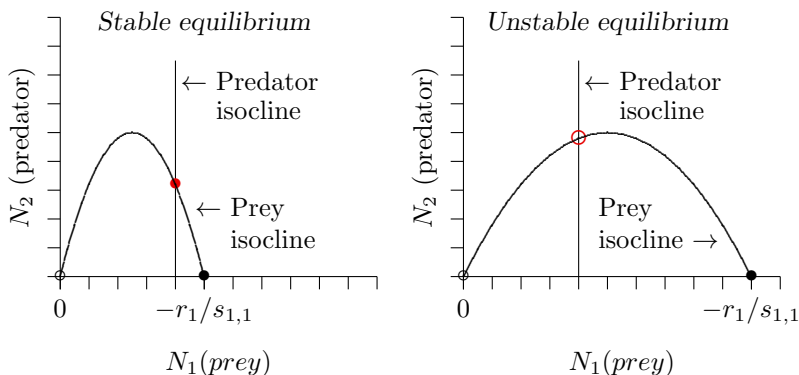
Similarly, where does the predator growth,  $1/N_2 \, dN_2/dt$ , cease for the same phase-plane? Let's follow similar algebra:

$$\begin{aligned}\frac{1}{N_2} \frac{dN_2}{dt} &= 0 = r_2 + s_{2,1} \frac{1}{N_1} \\ \Rightarrow -r_2 &= s_{2,1} \frac{1}{N_1} \\ \Rightarrow N_1 &= -\frac{s_{2,1}}{r_2}\end{aligned}$$

This predator isocline is simply a vertical line, as before in Figures 12.9 and following figures. But note that the prey curve has the form of an inverted parabola—a hump, as graphed for two cases in Figure 12.17.

Remarkably, this formulation of predator–prey equations closely matches what earlier researchers deduced logically and graphically, when computers were slow or not yet available. If you want to better understand the shape of the prey curve, read Rosenzweig's 1969 paper entitled “Why the prey curve has a hump.” For interest, his hand-drawn published figure with experimental data points is reproduced in Figure 12.18.

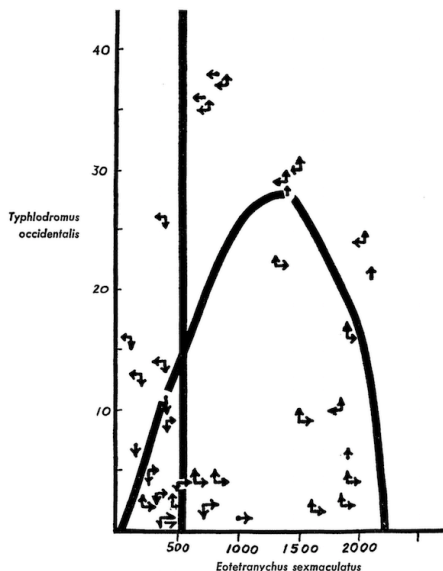
Rosenzweig pointed out a paradoxical effect, which he called “the paradox of enrichment.” At left in Figure 12.17, the prey have a relatively low carrying capacity, with  $K = -r_1/s_{1,1}$  about halfway along the horizontal axis. If you analyze the flow around the red dot that marks the equilibrium point to the right of the hump, or run a program to simulate the equations we just derived, you will find that the populations spiral inward. The equilibrium is stable.



**Figure 12.17.** *The paradox of enrichment, Rosenzweig, AmNat 1969.*

The paradox is this: if you try to improve conditions for the prey by increasing their carrying capacity—by artificially providing additional food, for example— you can drive the equilibrium to the left of the hump, as in the right part of Figure 12.17. Around the equilibrium marked by the red circle, the populations spiral outward. The system has become unstable.

This is a warning from ecological theory. In conservation efforts where predators are present, trying to enhance a prey population by increasing its carrying capacity could have the opposite effect. This is not to say that efforts to enhance prey populations should not be undertaken, only that they should proceed with appropriate caution and study.



**Figure 12.18.** Rosenzweig’s original 1969 graph with phase-space arrows, interpreting Huffaker’s 1958 experiments with mites.

## 12.8 Effects of space

In predator–prey systems, especially in confined areas, the predator tends to capture all the prey and then starve, so the systems “crash.” But over large areas it is conceivable that a predator can completely wipe out its prey in one area and not go extinct, because it can simply move to another area where the prey still exist. Prey can then repopulate the area from which they had been depleted.

Imagine a series of interconnected cells where, with some restrictions, predator and prey can migrate between adjacent cells. Now, even though the system may be locally unstable and crash in individual cells, the entire system across all cells could be stable and persist indefinitely.

In the 1930 the Russian ecologist Gause conducted a very famous set of early experiments on competition among protozoa, but he also studied predation of *Didinium* on *Paramecium*. The populations he set up would commonly crash and go extinct, with the *Didinium* eating all the *Paramecia* and then finding themselves without food. If he made places for the *Paramecium* prey to hide, however, the systems could persist for many cycles.

In the 1960s Krebs noticed that populations of fenced mice, even those with a full half-acre within the fence, would crash and disappear after grossly overgrazing their habitat. But in areas where they were allowed to disperse, the populations would persist.

Huffaker also ran extensive experiments, again in the 1960s, with mites and oranges. A single population of mites on a single orange would crash and the whole population would disappear. Using multiple oranges with limited migration paths between them, however, allowed the system to persist for many generations.

And in the 1970s Lukinbill did similar work with protozoa in aquatic tubs—larger and larger tubs holding miniature predator–prey systems. He found that the larger the tub, the longer the system persisted.

The point to remember here is that the mere presence of spatial structure, in one form or another, can allow a predator–prey system to persist. The basic reason is simply that species can go extinct in some areas while continually re-colonizing other areas, always maintaining a population that blinks in and out locally, but persists globally.



## Chapter 13

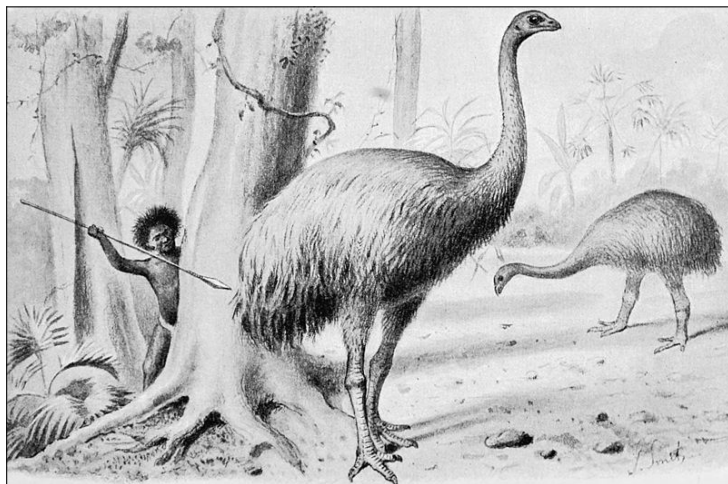
### Humans as predators

Early humans suffered from predators just as other primates suffer still. Eventually, though, they developed spears longer than the longest teeth and became one of the top predators on land. Even if they did not eat sabre-tooth tigers, they were able to kill them. We know from vivid paintings on rock walls in the protected shelter of caves that our ancestors at least fancied themselves as hunters (Figure 13.1).

Humans are now the dominant large vertebrate on the planet. But on all the continents beyond Africa, large vertebrates were prominent in the ecosystems before our ancestors arrived. In Africa many remain, coevolved with humans and perhaps wiser to our ways. Elsewhere, however, they had little fear when our ancestors arrived (Figure 13.2).



**Figure 13.1.** *Hunter and hunted.*



**Figure 13.2.** *Artist's conception. The Moa had no clue that the diminutive primate was aiming a barb that would shortly pierce its heart. Unafraid and then gone.*

The reasons behind the extinction of so many megafauna are controversial. Archeologist Haynes and others believe humans are responsible. Archeologist Grayson and others blame climate change, though animals had been through many glaciations and deglaciations before. Mammalogist MacPhee and virologist Marx postulate a virulent “hyper-disease” brought by humans. And geologist Kennett and colleagues assign a comet impact as the cause—an interesting theory, as some major human hunters disappeared at about the same time as the larger mammals.



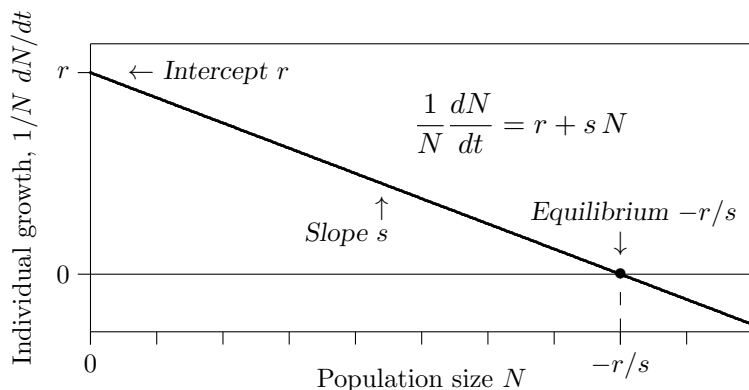
**Figure 13.3.** *The remaining mass of Earth's megafauna lives in the sea.*

In any case, when something extreme happens, several causes may be working in concert. We do know from historical records that only about one human lifetime ago our predecessors in North America hunted bison almost to extinction (Figure 12.3). Now the large remaining populations of megafauna are in the seas. What is their fate?

### 13.1 Consciously controlled predation

Consider predation by humans that is not subject to the cyclical dynamics of natural predator–prey interactions, but is instead consciously controlled to provide steady, reliable returns—from the world’s fisheries, for example. How is this attempted?

Recall logistic population growth, where the ecological term  $s$  is negative. Figure 13.4 shows the individual growth rate on the vertical axis and the population density on the horizontal axis, as you have seen before. Individual growth means the same thing as growth per capita, or relative growth, or percentage growth if multiplied by 100. The intention is to apply this to logistically growing populations of prey.



**Figure 13.4.** Logistic population growth, individual rate.

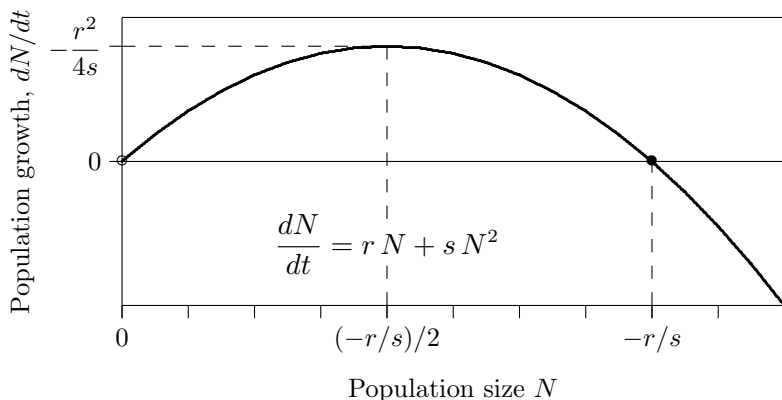
It is the growth rate of the whole population, however, that is of interest in controlled predation—not the per capita growth rate—since it is a fraction of the whole population that is to be taken. So the vertical axis should show  $dN/dt$  rather than  $1/N \, dN/dt$ . Start with the individual growth rate, which reaches its maximum  $r$  as  $N$  approaches 0. Here the population produces very few individuals, because the population itself is almost nonexistent.

$$\frac{1}{N} \frac{dN}{dt} = r + s N.$$

The goal is to maximize the population growth rate so that the greatest number of prey can be taken. To find that number, multiply both sides of the equation above by the number of individuals,  $N$ , to get the growth rate of the entire population—in other words, to determine how many individuals are added to the population in a unit of time. The result is

$$\frac{dN}{dt} = r N + s N^2$$

The growth of the entire population,  $dN/dt$ , has the shape of an inverted parabola, shown in Figure 13.5, since  $s$  is negative. Population growth is lowest when the population is very small, near 0, or when it is high, near its carrying capacity,  $-r/s$ . It reaches its maximum growth rate midway, at half the carrying capacity,  $(-r/s)/2$ . So if the population is kept at half its carrying capacity, it will be growing its fastest and the greatest amount can be “harvested” each year.



**Figure 13.5.** Logistic population growth, population rate.

What is that maximum rate? To find it, substitute half the carrying capacity,  $-r/(2s)$ , for  $N$  in the equation above, giving

$$\begin{aligned}
 \left. \frac{dN}{dt} \right|_{\max} &= r \left( -\frac{r}{2s} \right) + s \left( -\frac{r}{2s} \right)^2 \\
 &= -\frac{r^2}{2s} + s \frac{r^2}{4s^2} \\
 &= -\frac{r^2}{4s}
 \end{aligned}$$

So in this theory the population grows most rapidly at rate  $-r^2/(4s)$ , producing the greatest number of new individuals if drawn down to half its carrying capacity. This has been called the “maximum sustainable yield.”



**Figure 13.6.** *Fishing then and now.*

Let us introduce a harvesting intensity,  $H$ . When  $H$  is zero, there is no harvesting, and when  $H$  is 1, harvesting is at the maximum sustainable rate. In between it is proportional.

$$\frac{dN}{dt} = (rN + sN^2) + H \frac{r^2}{4s}$$

↑

↑

↑

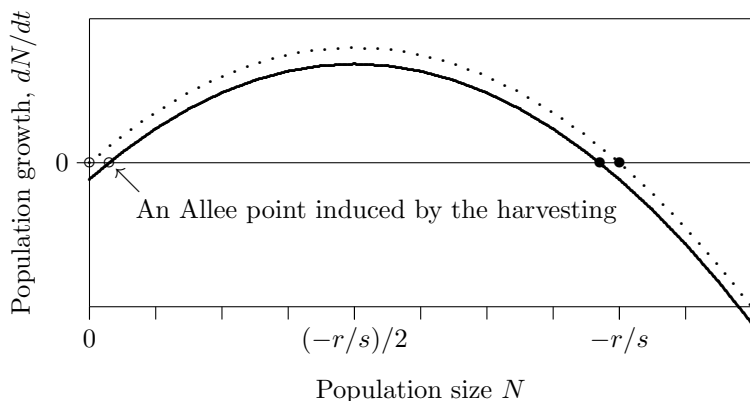
The rate of removal: the number of individuals caught per time

unit

The rate of addition (in parentheses): the number of individuals born per time unit minus those dying from causes other than hunting

The net rate of population growth: the number of individuals per time unit, considering births, deaths, and hunting

If individual fishermen predominate (Figure 13.6, left),  $H$  will be small. This pulls the curve down, as in Figure 13.7, lowering the carrying capacity slightly and leaving somewhat fewer fish in the sea. It also introduces an Allee point, though



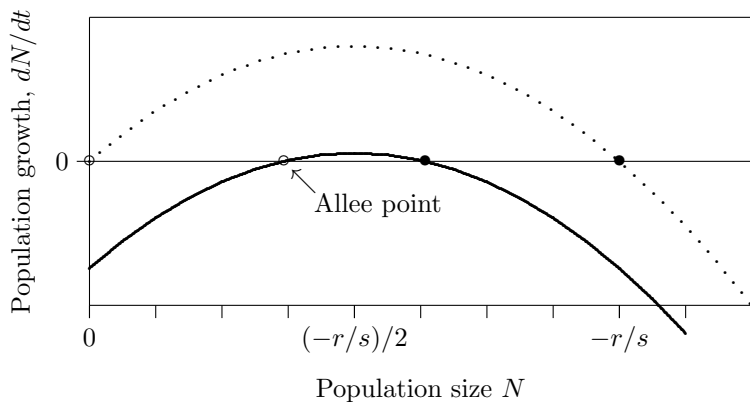
**Figure 13.7.** Population growth with light harvesting ( $H$  small).

that point is far below the equilibrium and therefore not a significant danger.

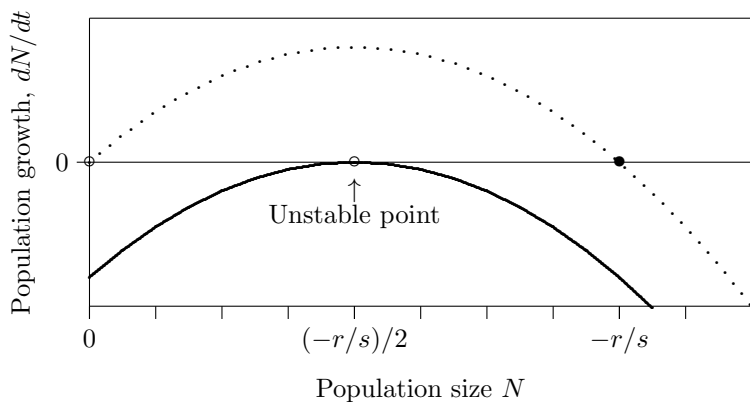
But with increasingly focused and mechanized fishing (Figure 13.6, right),  $H$  approaches 1 and the curve is pulled farther down (Figure 13.8). The carrying capacity is markedly reduced and the population produces new individuals at a large rate. And the Allee point is pulled close to the carrying capacity, introducing a danger that unforeseen fluctuations in the population could push the population below the Allee point and collapse the fishery.

Finally, with hunting or fishing at the maximum sustainable yield, the Allee point coincides with the carrying capacity and in effect annihilates it (Figure 13.9). This introduces a dynamical conflict because there is a stable situation to the





**Figure 13.8.** Population growth with heavy harvesting ( $H$  near 1).



**Figure 13.9.** Population growth with maximal harvesting ( $H = 1$ ).

right but an unstable one to the left, making it inevitable that the population will fall below the Allee point and collapse. The maximum sustainable yield is not sustainable!

## 13.2 Stochastic modelling

Program 13.4 simulates harvesting at the so-called maximal sustainable yield. It introduces small random fluctuations in the population—so small that they cannot be discerned in a graph. The slight stochasticity makes the program take a different trajectory each time it runs, with widely different time courses. Inevitably, however, the populations drift below the Allee point and rapidly collapse, as in the sample run of the program shown in Figure 13.10.

In the age of sailing, at the arrow marked A, fishing was high-effort but low-impact and fisheries stayed approximately at their carrying capacity,  $K$ . “Optimal harvesting” was introduced once mathematical ecology combined with diesel technology, and fisheries helped feed the growing human and domestic animal populations, with fish populations near “maximum sustainable yield,” as expected. But throughout the 20th century, as shown on either side of the arrow marked B, fish populations continued to decline, and before 2015—at the arrow marked C—it becomes clear that something is seriously amiss.

```

# SIMULATE ONE YEAR
#
# This routine simulates a differential equation for optimal
# harvesting through one time unit, such as one year, taking
# very small time steps along the way.
#
# The 'runif' function applies random noise to the population.
# Therefore it runs differently each time and the collapse
# can be rapid or delayed.
#
# ENTRY: 'N' is the starting population for the species being
#         simulated.
#         'H' is the harvesting intensity, 0 to 1.
#         'K' is the carrying capacity of the species in question.
#         'r' is the intrinsic growth rate.
#         'dt' is the duration of each small time step to be taken
#              throughout the year or other time unit.
#
# EXIT:   'N' is the estimated population at the end of the time
#         unit.

SimulateOneYear = function(dt)
{ for(v in 1:(1/dt))
  { dN = (r+s*N)*N - H*r^2/(4*s)*dt; # Advance the time step.
    N=N+dN; } # Compute the change.
  if(N<=0) stop("Extinction"); # Update the population value.
  assign("N",N, envir=.GlobalEnv); # Make sure it is not extinct.
                                     # Export the results.

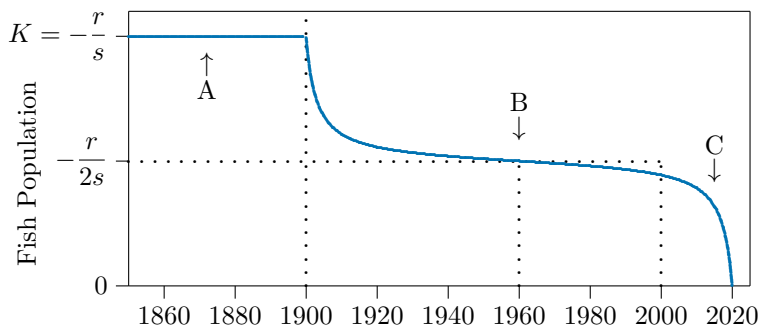
r=1.75; s=-0.00175; N=1000; H=0; # Establish parameters.

for(t in 1850:2100)
{ if(t>=1900) H=1; # Advance to the next year.
  print(c(t,N)); # Harvesting lightly until 1900.
  N = (runif(1)*2-1)*10 + N; # Display intermediate results.
  SimulateOneYear(1/(365*24)); } # Apply stochasticity.
                                     # Advance the year and repeat.

```

**Program 13.4.** *This program simulates maximal harvesting with small fluctuations in the populations.*

What happened? A collapse is part of the dynamics of this kind of harvesting. Inevitable stochasticity in harvest combines unfavorably with an unstable equilibrium in the prey population. In some runs it collapses in 80 years, in others it may take 300. The timing is not predictable; the main predictable property of the simulation is that ultimately the system will collapse.



**Figure 13.10.** One sample run of Program 13.4, showing the collapse typical of such runs.

### 13.3 Present situation

Many of the world’s fisheries are under collapse, and in the oceans we seem to be on a path like the one our predecessor predators took on land.

There are better ecological approaches—a “constant effort” approach, for example, rather than the “constant harvest” examined here—but economic, social, and political pressures have kept them from extensive use.

We hope this chapter has shown you that insufficient examination of ecological equations applied on a large scale can generate disasters, that equilibria must not be considered apart from their stability, and that management of real ecological systems requires attention to natural history and social conditions.



**Figure 13.11.** *Excruciatingly efficient modern methods of fishing.*

## Chapter 14

### Humans as prey

Our species no longer suffers large predators as so many species do (Figure 13.1). But dangerous predators remain part of the human condition. We call them diseases.

By analogy, think of visible organisms living in a pond—from birds, fish, frogs, insects, and plankton to aquatic plants (Figure 14.1, left). To be successful across a region, the organisms must gain resources in the pond while competing with other species, survive predators, and enable their offspring to disperse to another pond. To be successful they must not destroy the pond in which they live, at least until they or their offspring have dispersed to another pond.



**Figure 14.1.** *Macroscopic organisms living in a pond are analogous to microscopic pathogens living in a body.*

What is the body of a plant or animal to an infectious virus or bacterium? It is like a pond. There may be other pathogens in the body competing for its metabolic resources. There are predators in the body in the form of an immune system. And to be successful the pathogen must disperse to another body without destroying the body in which it lives, at least until it or its offspring has orchestrated a way to disperse into and colonize another body.

## 14.1 Portals

A pond has entry and exit portals. If an organism is small enough, it can exit a pond on wind and spray. Some organisms can float downstream to another pond, while birds and insects can simply fly. Larger organisms such as amphibians can hop or walk from pond to pond to lay eggs. And a new exit portal has recently appeared in the form of boats and trailers that carry invasive weeds and animals from one pond and deposit them in another.

Think analogously of the entry and exit portals of an animal (Table 14.1). How can pathogens leave one body and enter another? While skin covers at most two square meters in humans, mucus membranes of the respiratory, digestive, and reproductive tracts cover more than 400 square meters. So, mucus membranes become good portals.

Successful diseases can exploit obligate behaviors. Animals, for example, must breathe continually, so exploiting the respiratory pathway—being breathed out into the air by one animal and breathed in by another— is a reliable and ever-present method of transmission.

**Table 14.1.** *How infections can leave and enter the body (mix and match).*

**Portals of exit:**

Breath

Droplets (sneezing, coughing)

Saliva

Sweat

Tears

Feces

Urine

Seminal fluids

Vaginal fluids

Blisters, boils, zits (via scratching, breaking the skin)

Blood (mosquitoes, ticks, hemorrhage)

**Portals of entry:**

Blood (cuts, wounds, insects, needles)

Lungs

Nose

Eyes (conjunctivia)

Mouth (mucosa)

Mouth (tooth/gingivia junction)

Gut

Skin (scabies, triconosis, warts, etc.)

Urinary tract

Rectum

Vagina (mucosa)

Penis (mucosa)



Animals must also eat frequently and periodically, so exploiting the oral pathway—leaving through urine and feces and getting back through the alimentary canal—is another reliable path, at least under conditions in the wild or with animals that live on and eat grass (Figure 14.1, right).

Animals must reproduce, so exploiting the genital pathway—where many animals come into direct bodily contact—is a third reliable path. This can be especially productive, as mucosal tissues of high surface area are touching and infected fluids can be transferred from one sex to another. A pathogen that can get into seminal fluid of a mammal, for example, has a direct path for transmission.

Finally, many animals care for young, so exploiting parental care can be a fourth reliable path. A pathogen that can enter a mother's milk has a direct path for infecting her offspring. Such transmission from parent to offspring is called “vertical transmission,” with other forms called “horizontal transmission.”

## 14.2 Pathogen mobility

While microscopic pathogens are not independently mobile, their hosts are, and pathogens have evolved ingenious ways of modifying the behavior of a host to enable their transferal to another host.



**Figure 14.2.** *Tiny predators getting from one host to another*

Sneezing and coughing reflexes, for instance, are ancient responses for clearing obstructions from the nose and throat, and some pathogens deceptively induce those responses for a pathway out (Figure 14.2).

What we call “symptoms of disease” are not, then, random effects of a disease, but can often be a pathogen’s way of getting out of one pond, so to speak, and into another. Any of the pathways of Table 14.1 can be exploited by a pathogen, which in doing so may upset these pathways and cause the host great distress.



**Figure 14.3.** *Pink Eye and Cold Sores.*

Some pathogens, for example, get into your eyes and tears and deceptively cause itching and soreness (Figure 14.3, left), inducing you to rub your eyes and transfer the pathogens to your fingers. This in turn can successfully move them to other locations like food, from which they can enter another host by the oral pathway.

Others pathogens are able to break the skin and get out of the body on their own. Cold sores (Figure 14.3, right), a form of oral herpes, form around the mouth and nose, transmitting to what touches the sore. A related genital herpes is transmitted sexually, though evolution has been proceeding and the genital form is now able to infect orally and the oral form genitally. This and other sexually transmitted diseases have been increasing since about the middle of the twentieth century.

One of the most successful pathogens to use the lungs and skin as pathways out of the body is smallpox★ (Figure 14.4). It leaves its host with permanent scars, often over the entire body. Smallpox is an ancient disease, dating from the



**Figure 14.4.** *Smallpox, the first disease consciously driven extinct from the natural world.*

time before the pyramids, that can kill a majority of those it infects and at times can infect a majority of the population.

The very success and horror of smallpox was part of its ultimate destruction—its eradication was the first complete victory in the conquest of disease. Thanks to prolonged diligent attention throughout the world, and of course to the invention of vaccine, smallpox has been made extinct in the natural world. (We say “natural world” because laboratory samples are being retained.)

William Foege,★ a key player in orchestrating the extinction of smallpox, said that we can conquer disease because we evolve so much more rapidly than the disease. This may be startling to hear, given that our physiological evolution

is much slower than that of viruses or bacteria. But, he explained, because we evolve socially much more rapidly than a disease can evolve biologically, we are able to “outsmart” the disease.

Rinderpest,★ a viral disease causing high rates of mortality in cattle and wild mammals, was the second disease declared extinct in the natural world. Others—such as polio★ and Guinea-worm disease,★ — may soon follow, though the latter may simply be eradicated from human populations by our continual isolation from sources of infection.

Diseases can exploit blood-sucking parasites to move directly from the blood stream of one host to that of another. Lyme disease (Figure 14.5, left), for example, is spread by ticks, which puncture the skin to obtain a blood meal for themselves but in the process can transfer pathogens. And Ebola (Figure 14.5, right) leaves by almost every exit portal listed in Table 14.1, destroying those portals by carrying not just the pathogen but chunks of lung, intestine, or skin in the process.



**Figure 14.5.** *Lyme disease (left) and one form of Ebola (right).*

Human populations are so large and dense that even relatively inefficient pathogens can be successful. And diseases, of course, also affect wild and domestic animals as well as crops and other plants.

As the next chapter illustrates, many diseases can evolve to be relatively harmless to their hosts, promoting transmission and allowing the disease to become widespread. Rust fungus infections, for example, are common in many plant species, but seldom lead to the death of the host. Powder mildew on the prairie plant *Monarda fistulosa* is so widespread that it is used in plant identification books as a way to identify the species (Figure 14.6 right).

Pathogens can dramatically alter animal behavior. Rabies first gets through the salivary glands and into the saliva of an infected host. Physiological changes then make the host animal salivate profusely—foaming at the mouth—while psychological changes make it appear crazy and angry. The animal



**Figure 14.6.** *Prairie Bush Clover* and *Monarda fistulosa*.

then bites through the skin of another animal, transferring the pathogen to that animal's bloodstream, and the cycle continues. Both the physiological and psychological changes are caused by the pathogen and allow it to spread, even after the death of the initial host.

“Mad dog behavior” is thus not an accidental consequence of the disease, but precisely the means the pathogen has developed for getting, so to speak, from pond to pond.

**I**t is useful to try to think of all the ways a pathogen might alter the behavior of its host to force the host to transfer the pathogen. This is not just an intellectual exercise, but could help identify potential for new emerging diseases. For example, what should a sexually transmitted disease do to its host in order to spread faster? It should render its host more active sexually! And indeed this happens. Female chimpanzees would normally mate only every two years or so, after having given birth and nursed their young to the point of weaning. But female chimps infected with SIV★ (simian immunodeficiency virus) reach estrus every month or so, and do not

conceive. The pathogen changes their mating behavior to spread itself more than an order of magnitude faster than it would otherwise spread.

Inspired to think in this way, one student came up with a novel idea: Imagine a disease that can escape through the sweat glands without harming its host. As behavioral modification, it makes infected hosts want to undergo strenuous exercise in groups, such as in gymnasiums—thus explaining the entire modern exercise phenomenon as a disease! (Gerbils may also harbor this disease.)

### 14.3 Disease more generally

The tiniest predators—infection and disease—differ from what are usually thought of as predators in a number of ways, some of which you have seen. First, the disease organism is much smaller than its victim and not independently mobile. It must be carried by wind or water, or induce its host to transfer it in one of numerous ways.

Second, disease does not necessarily kill its victims. Many diseases, in fact, leave their victims largely intact, the better to transmit the pathogen to another host.

And third, after infection, the prey may become forever immune to future infections, both by that pathogen and related ones. This immunity is created by the enormously elaborate “immune system”★ of vertebrates and other animals—a system recognizing and killing incoming pathogens before they can incubate and do much harm, and as elaborate and complex as the brain and central nervous system.



One of the great discoveries of the last millennium was that the immune system could be primed to recognize a pathogen before it invaded, though what was happening inside the body was not understood until the twentieth century. Vaccination★ played a central role in the eradication of smallpox. The twentieth century also saw the discovery of antibiotics such as penicillin, which allow doctors to cure disease after an infection has progressed.

These discoveries show us that humans must be considered separately from plants and other animals, for we have developed special powers against disease. We are not passive prey, and do not simply suffer a disease or make behavioral modifications to avoid it. Instead we actively and globally strive to destroy disease, or subdue it. And we extend these efforts to diseases affecting the animals and plants we depend on.

With respect to disease, plants have distinct properties that are in direct contrast with those of animals. Animals, in general, are high-energy organisms—metabolizing rapidly, moving about, and perpetually pumping oxygen throughout the body. Plants are nothing like this. Rather than hearts and rapid fluid flow to distribute food and oxygen and to cleanse waste materials, plants use the passive effects of capillary action★ and evaporation. This requires the tiniest of veins, or capillary action will fail. And these veins are too small to transport plant cells, or to allow larger pathogens like protozoa and many bacteria to gain access to the entire organism. This also means that plants cannot have the

same kind of immune system as animals, with their own cells travelling through their tissues on patrol.

In addition, plants are typically modular. An infected part—leaf, flower, or whole limb—can be discarded and grown again. The apical meristem★ cells at the tips of branches and roots are capable of developing entirely new plants. While cancer cells can spread through the body of an animal and kill it, such cells would simply plug the veins of plants. So while animals get cancer, plants get cankers. Plants have longevity, while animals have mortality—the cost of being a high-energy organism.

## 14.4 The strange case of polio

Polio had long been a relatively rare disease of infants, called “infantile paralysis.” In the middle of the twentieth century, however, it became more common and started affecting older children and adults. A new form of the disease seemed to be emerging.

Which of these people, do you think, performed the greatest service to human health and hygiene in the twentieth century, but inadvertently triggered this mid-century polio epidemic? (a) Louis Pasteur, discoverer of pasteurization, (b) Alexander Fleming, discoverer of penicillin, (c) Jonas Salk, creator of the polio vaccine, (d) Franklin Delano Roosevelt, President of the United States and polio victim, or (e) Henry Ford, creator of the production line.

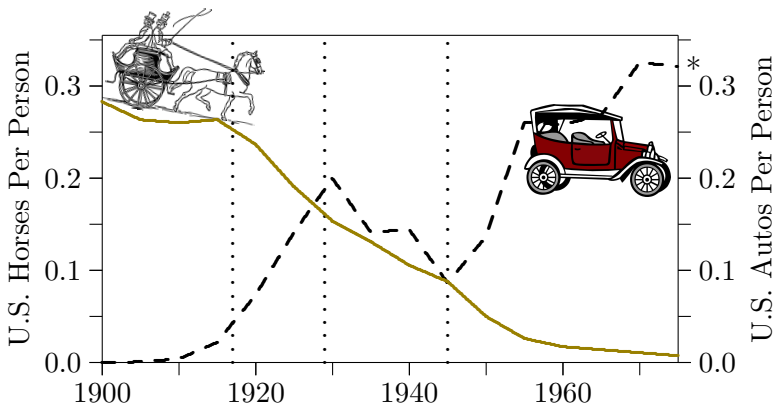
This seems a strange question, with industrialist Henry Ford under consideration. But indeed, the answer is Henry Ford!★ At the beginning of the twentieth century, most local

transportation was by horse and powered, of course, almost entirely by the biofuel hay. While it has now largely left social memory, in the early decades of the twentieth century the streets were a slurry of gravel and horse manure. Flies were everywhere, and caused little concern paid, for this was the norm. People's outhouses were ventilated to the open air, and flies laid eggs there and in the streets, then freely entered houses and landed on food. A number of diseases take advantage of the fecal–oral pathway, and polio is one of them.

But automobiles and tractors intervened. As the horse-drawn era closed, manure generally vanished, running water arrived and flush toilets arrived, hygiene improved, sealed screen doors became common, and flies died in vast numbers. Without intending it, Henry Ford became the greatest fly killer of all time. The availability of the fecal–oral pathway diminished, and the infectivity of related diseases fell.

Figure 14.7 shows the horse population declining slowly until World War I, then falling rather steadily as the number of cars increased in stages. The first increase in the number of cars ended around 1930 with the Great Depression, when many people could not afford cars. The end of World War II in 1945 brought another boom in car purchases, and by 1975 society had replaced almost every horse per capita with a car.

As the chance of catching polio fell, the average age of catching it increased. To understand this, consider residents of the northern hemisphere living at various latitudes. Because residents of the High Arctic have a chance to see the



\* Cars per person calculated from yearly data for U.S. car production, assuming an eight-year average life for a car.

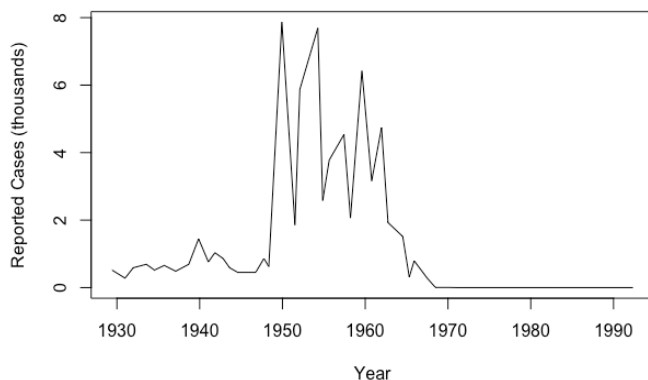
**Figure 14.7.** *Horses and estimated cars in the United States, the source of Henry Ford's public health legacy.*

northern lights—the aurora borealis★—every week, children living there will likely see the aurora before their first birthday. Farther south, at 50 degrees north latitude, the aurora may appear only once every few years, especially near the lights of cities, so a child could be 5 or 10 years old before ever seeing it. And finally, say at 35 degrees north latitude, the aurora may appear but once or twice in a lifetime, so many people could be in middle age before viewing them, and others might go an entire lifetime without being touched by their hypnotic display.

So it is with disease. The number of opportunities for catching a highly infectious disease, naturally, is high. If the quantity of pathogens in the environment is such that all individuals encounter them on average once a year, only about one-third of infants will avoid infection in their first year. (Actually the number is  $1/e = 0.367\dots$ , if the chance of infection is completely random.) The same fraction of the remaining infants will catch the disease during their first year, and the rest will be age two or older when they catch the disease. Therefore, as the pathways for transmitting polio diminished during the twentieth century, the chances of catching it in any year decreased and the age of onset correspondingly increased.

Polio is like some other diseases that are not usually virulent in infants and young children. A baby infected with polio might have a cold and a runny nose, and the infection might go without particular notice. In an older child, however, it can stop bone growth and muscle development, crippling the child. The polio epidemic of mid-century America was thus not a new disease emerging, but an ancient disease dying out.

Albert Sabin,<sup>★</sup> of polio vaccine fame, suspected a connection with flies. In 1941 he and his colleagues reported in *Science* on a study they performed in areas of the United States where polio had struck. They captured flies, pureed them in sterile fluid, and gave them to monkeys in feedings, nosedrops, or injections. As they put it, “Down came the monkeys with polio.”

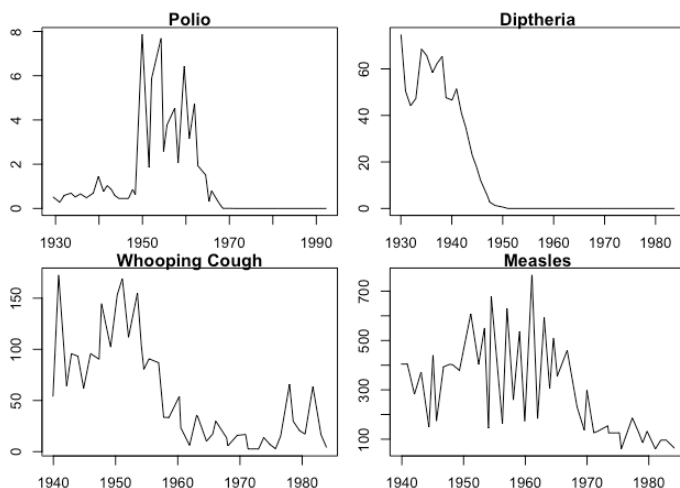


**Figure 14.8.** *The recent course of polio in the United States.*

With further improvements in hygiene and broad use of vaccines, rates of polio have dropped to nearly zero. Figure 14.8 shows a moderate number of cases of polio before the late 1940s, an outbreak lasting until the early 1960s, nearly nothing in the years following.



**Figure 14.9.** *Tillie and Oscar Lehman's adz-hewn log cabin with frame addition, circa 1930s—the end of the horse-drawn erait. They raised ten children in this cabin, all of whom likely had polio unnoticed as infants.*



**Figure 14.10.** *Paths of four diseases. Vertical axis shows cases in thousands.*

## 14.5 Modern disease trends

Many ordinary diseases have been subdued since the last half of the twentieth century, some to the point of extinction from the natural world. Smallpox and rinderpest are gone, and polio nearly so—as we are writing this (2016–17), polio workers are anticipating its extinction in the foreseeable future. Diphtheria is on a similar path (Figure 14.10), with no cases at all in the United States during the twentieth century.

Diseases such as whooping cough and measles (Figure 14.10) have been subdued but remain with us, with some cycling

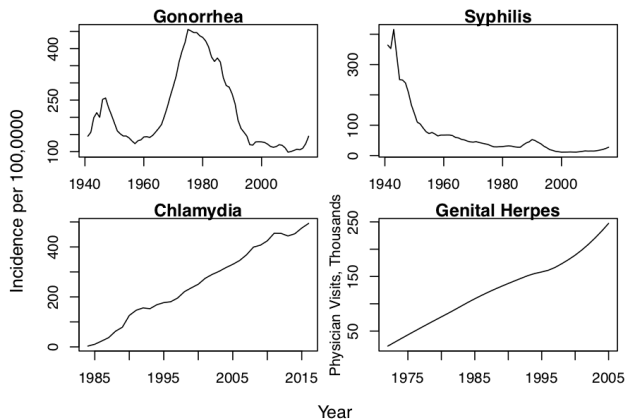


through periodic outbreaks. The rates of many ordinary diseases are being reduced, and infectious disease is no longer the major cause of deaths in human populations.

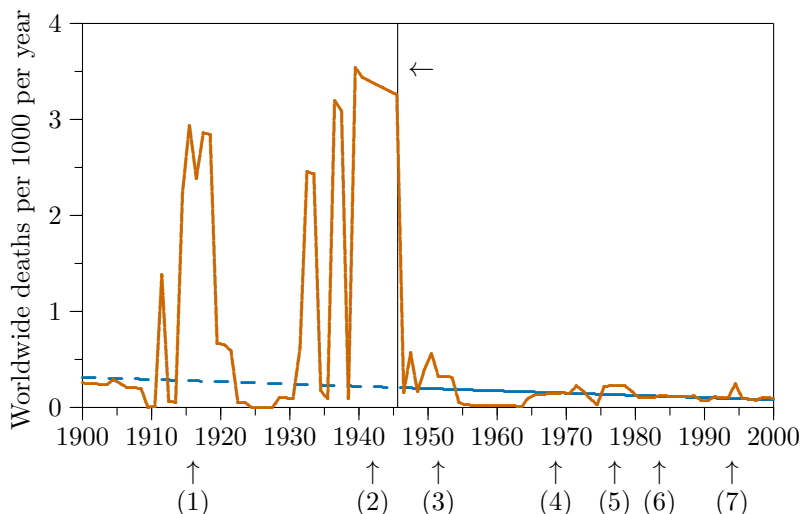
Rates of various sexually transmitted diseases, however, are on a different course (Figure 14.11). Gonorrhea rates have declined but remain considerably above zero, and it is a commonly reported disease in the United States. The appearance of syphilis appears to be cyclic, as rates had declined but are now rising again. Rates of chlamydia—which can lead to serious outcomes, including infertility in women—have been increasing steadily, without an end in sight, and rates of genital herpes and other sexually transmitted diseases are rising similarly. Sexually transmitted diseases are a prominent problem to be solved in the twentieth century.

## 14.6 An ancient plague perhaps vanishing

We close this chapter with a graph to ponder. Examine Figure 14.12, an epidemiological view of annual deaths per 1000 population during the twentieth century, from a widespread and ancient cause. Imagine what it represents. Is it a sexually transmitted disease, an ordinary disease with an effective treatment introduced around 1946, or something else entirely?



**Figure 14.11.** Sexually transmitted diseases in the U.S. The vertical axis shows the rate per 100,000 population.



**Figure 14.12.** *Worldwide deaths per year from an ancient human malady.*

The solid blue regression line goes through the average number of deaths over time from 1946 forward, projected back on the dashed line through the outbreaks earlier in the century.

Figure 14.12 is actually an epidemiological view of deaths from warfare, which have been declining per capita over the past 70 years. The vertical line marks the beginning of the atomic era, and the numbers in parenthesis indicate (1) World War I, (2) World War II, (3) Korea, (4) Vietnam, (5) Cambodia and Ethiopia, (6) USSR–Afghanistan and Iran–Iraq, and (7) Rwanda.

Why include a chart of war deaths in a book on ecology, and in a chapter on the ecology of disease? First, war is directly connected with ecology and the environment. Throughout human history, warfare has been caused by environmental change, as existing territories became unproductive and new territories were sought, and in turn it has caused environmental change through habitat alteration and other forces. Second, humans are a dominant ecological force, whose impact we examine in this book, and warfare has been a prominent theme in the human condition. And third, warfare has some of the properties of a disease. It can spread from places of origin like a disease, and has analogs of competitors and mutualists in addition to obvious roles of predators and prey. Moreover, it involves an infectious agent—replicating not as biological agents spread between bodies of their hosts, but abstractly, like ideas—as seen by Richard Dawkins,★ — replicate as memes between minds of their hosts.

Warfare has enough abstract similarities to biological agents, and enough tangible effects on ecology of the planet, that we want to offer these ideas for your future consideration, and

with the hope that some progress can be made by enough minds examining them.

From discussions with students and colleagues thus far, and from parts of the literature, here are some thoughts for your consideration.

*Nuclear weapons.* It seems indisputable that these caused an initial collapse in warfare, but they may also have affected the number of war deaths during the rest of the century. Of course, they could have led to unprecedented numbers of deaths had political arrangements worked out differently.

*Immediate journalism.* Photographic news coverage becoming ever more immediate gave the world a different view of war. Cell-phone cameras, social networks, and the internet expand that indefinitely today.

*International law.* Most international law may not yet be written, but we have seen its beginnings. How much has the encoding of war crimes since World War II contributed to the decline?

*Self-government.* The rapid expansion of self-government since the middle of the twentieth century may have contributed to the decline in war-related deaths, as self-governing nations tend to avoid war with other self-governing nations.

*International trade.* In the same way, nations that trade mutualistically may also tend to avoid war so as to avoid destroying trading partnerships.

*Expanding ethics.* At the end of 1957 the Soviets launched the space dog “Little Curly” into orbit, intending him to

die while orbiting our planet. Though this went largely unchallenged in the twentieth century, would any nation be able to do something like this in the twenty-first? Do expanding ethics in other realms contribute at all to the decline in war deaths?

*Women in power.* It is worth considering whether the increasing proportion of women in government has an effect on the number of war-related deaths. Among primates such as chimpanzees and baboons, males are the more aggressive sex. If this is true in humans, might it have continued effects in the future?

*Improved medicine.* Serious wounds once meant infection and death, but now victims can recover. And mortality from diseases which can spread rapidly in wartime—like influenza—has been reduced. The same level of warfare now manifests fewer deaths, making part of the decline an artifact.

*Reduced overkill.* The percentage of a population killed during a war decreased from nearly 100% in some ancient times to “what is necessary” in more recent cases. Has the development of precision weaponry contributed to continuing decrease in war deaths? This would also make part of the decline an artifact.

**H**umanity has already unexpectedly broken the millennia-long rush of ever-accelerating population levels (Figure 6.3). Could something similar be happening with the millennia-long scourge of war? According to projections along the regression line, and for whatever the reasons, if the trends

of Figure 14.12 are real and can be understood and continued, humanity may be on a path toward the elimination of background warfare, even before the end of this century.

This material is a partial encapsulation of Steven Pinker's★ 800-page book, "The Better Angels of our Nature" (2011). That downward slope indicates a plausible goal to understand and a plausible hope to maintain. It is plausible, but we cannot know if it is practical without dedicating ourselves to it.

There is a level of self-fulfillment in such things, for if we collectively do not believe a goal like this can be achieved, it likely will not, but if we believe in it and work toward it, we might succeed. Along present trends, you can work with reasonable, rational, data-based hope to make background warfare vanish in your lifetime. And regardless of the outcome, all will be ennobled by the effort.

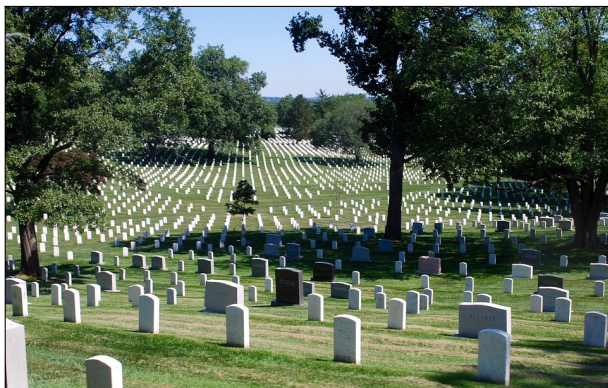


Figure 14.13. Arlington National Cemetery, Virginia.

## Chapter 15

### Theory of disease

#### 15.1 New terminology

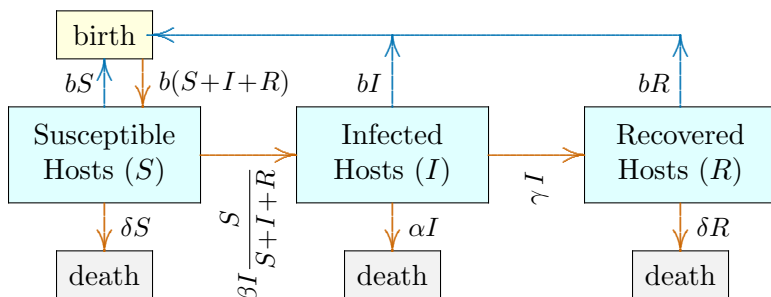
Terminology of the theory of disease is not completely consistent in the epidemiological literature, but we will use it consistently as follows.

*Virulence:* How much or how quickly a pathogen harms its host. Often symbolized as alpha,  $\alpha$ , in disease equations. Example: if one-tenth of infected organisms die in a particular time period, and everything is random,  $\alpha = 1/10$ .

*Infectivity:* How readily a pathogen arrives at and invades a new host. Often symbolized as beta,  $\beta$ , in disease equations. Example: in an otherwise uninfected population, if each infected host is expected to infect three others in a particular time period,  $\beta = 3$ .

*Basic reproductive number:* In an otherwise uninfected population, how many new infections an infected individual is expected to produce during the duration of the infection. Often symbolized as  $R_0$  in disease equations, and pronounced “are not.” This is a crucial number; if  $R_0$  is greater than 1, the disease will spread through the population, while if  $R_0$  is less than 1, the disease will die out.





**Figure 15.1.** Flow through an SIR system, a prototypical model of epidemiology.

## 15.2 The SIR flowchart

A standard starting point for examining the theory of disease is the “SIR model” (Figure 15.1). In this model individuals are born “susceptible,” into the box marked  $S$  at the left. They may remain there all their lives, leaving the box only upon their ultimate death—marked by the red arrow pointing downward from the box. The label  $\delta S$  on this arrow represents the rate of flow from the box—the rate of death of individuals who have never had the disease. The model assumes a per capita death rate of  $\delta$  deaths per individual per time unit. If  $\delta = 1/50$ , then one-fiftieth of the population will die each year. Multiplying by the number of individuals in the box,  $S$ , gives the flow out of the box,  $\delta S$  individuals per year.

The only other way out of the  $S$  box is along the red arrow pointing right, indicating susceptible individuals who become infected and move from the left box to the middle box. (The blue arrow pointing up indicates new individuals created by births, not existing individuals moving to a different box.) This rate of flow to the right is more complicated, depending not just on the number of susceptible individuals in the left-hand box but on the number of infected individuals  $I$  in the middle box. In the label on the right-pointing arrow out of the  $S$  box is the infectivity coefficient  $\beta$ , the number of susceptible individuals converted by each infected individual per time unit if all individuals in the whole population are susceptible. This is multiplied by the number of individuals who can do the infecting,  $I$ , then by the probability that an “infection propagule” will reach and infect someone who is susceptible,  $S/(S+I+R)$ . This is just the ratio of the number in the  $S$  box to the number in all boxes combined, and in effect “discounts” the maximum rate  $\beta$ . The entire term indicates the number of individuals per time unit leaving the  $S$  box at left and entering the  $I$  box in the middle.

All other flows in Figure 15.1 are similar. The virulence symbolized with  $\alpha$  is the rate of death from infected individuals—those in the  $I$  box. This results in  $\alpha I$  deaths per year among infected individuals, transferring from the blue  $I$  box to the gray box below it. Note that if infected individuals can also die from other causes, the actual virulence might be more like  $\alpha - \delta$ , though the situation is complicated by details of the disease. If a disease renders its victims bedridden, for example, their death rate from other causes such

as accidents, such as being hit by a train, may be reduced. Such refinements can be addressed in detailed models of specific diseases, but are best not considered in an introductory model like this.

The other way out of the blue  $I$  box in the middle of Figure 15.1 is by recovery, along the red arrow leading to the blue  $R$  box on the right. In this introductory model, recovered individuals are permanently immune to the disease, so the only exit from the  $R$  box is by death—the downward red arrow—with  $\delta R$  recovered individuals dying per year. Note that recovered individuals are assumed to be completely recovered, and not suffering any greater rate of death than susceptible individuals in the  $S$  box (both have the same death rate  $\delta$ .) Again, refinements on this assumption can be addressed in more detailed models of specific diseases.

The blue arrows represent offspring born and surviving, not individuals leaving one box for another. In this introductory model, all individuals have the same birth rate  $b$ , so that being infected or recovering does not affect the rate. The total number of offspring born and surviving is therefore  $b(S+I+R)$ . This is the final red arrow in Figure 15.1, placing newborns immediately into the box of susceptible individuals.

### 15.3 The SIR equations

The entire process depicted in Figure 15.1 is equivalent to the following set of equations.

$$\begin{aligned}\frac{dS}{dt} &= b(S+I+R) - \beta I \frac{S}{S+I+R} - \delta S \\ \frac{dI}{dt} &= \beta I \frac{S}{S+I+R} - \gamma I - \alpha I \\ \frac{dR}{dt} &= \gamma I - \delta R\end{aligned}\tag{15.1}$$

At the left in each equation is the net rate of change of each box, accounting for all arrows transferring individuals out of one box and into another. Again,  $S$  is the density of susceptible individuals,  $I$  the density of infected individuals, and  $R$  the density of recovered individuals. Note that the terms are balanced—the term  $\gamma I$ , for example, representing individuals entering the recovered box in the last equation, is balanced by the complementary term  $-\gamma I$ , leaving the infected box in the middle equation.

The SIR model is another “macroscale model.”★ With recent changes in computation, “microscale models,”★ processing tens or hundreds of millions of individual hosts, are becoming more widely used. They can reliably take you beyond what purely mathematical formulations can do. More about them in later chapters.

SIR is also a “frequency-dependent” model, at one end of a spectrum which has “density-dependent” models at the other end. Frequency dependence approximates situations in which infection propagules are limited, while density dependence approximates situations in which potential victims are limited.

But do not be concerned with the full SIR model for now. We shall simplify it here to reveal its basic properties. First, suppose there is no recovery—this is an incurable disease that, once contracted, stays with its victim forever. Many viral diseases approximate this situation—herpes and HIV, for example. In gray below are all the terms that will drop out if there is no recovery.

$$\frac{dS}{dt} = b(S+I+R) - \beta I \frac{S}{S+I+R} - \delta S$$

$$\frac{dI}{dt} = \beta I \frac{S}{S+I+R} - \gamma I - \alpha I$$

$$\frac{dR}{dt} = \gamma I - \delta R$$

Removing those terms gives an “SI” model.

$$\begin{aligned} \frac{dS}{dt} &= b(S+I) - \beta I \frac{S}{S+I} - \delta S \\ \frac{dI}{dt} &= \beta I \frac{S}{S+I} - \alpha I \end{aligned} \tag{15.2}$$

But we won’t be concerned with this model just now.

## 15.5 The I equation

We shall simplify the SI model further to an “I” model, the most basic epidemiological formulation. This can be done by considering a constant population, with births always matching deaths. To accomplish this, the birth term,  $b(S+I)$ , can be made equal to the death term,  $\delta(S+I)$ , giving

$$\begin{aligned}\frac{dS}{dt} &= \delta(S+I) - \beta I \frac{S}{S+I} - \delta S \\ \frac{dI}{dt} &= \beta I \frac{S}{S+I} - \alpha I\end{aligned}$$

However, since the total population—call it  $N$ —is constant,  $S$  is not needed in the equations at all. It is always equal to the total population  $N$  minus the number infected:  $S = N - I$ . You can forget about the  $S$  equation and substitute  $S = N - I$  into the  $I$  equation. This gives

$$\begin{aligned}\frac{dI}{dt} &= \beta I \frac{(N-I)}{(N-I) + I} - \alpha I \\ \Rightarrow \frac{dI}{dt} &= \beta I \frac{N-I}{N} - \alpha I \\ \Rightarrow \frac{dI}{dt} &= \beta I \left(1 - \frac{I}{N}\right) - \alpha I \\ \Rightarrow \frac{1}{I} \frac{dI}{dt} &= \beta \left(1 - \frac{I}{N}\right) - \alpha\end{aligned}$$

This is the beginning of the  $I$  model. It needs a little more work before proceeding with its analysis, but first some additional terminology:

*Infection:* A term applied as soon as a pathogen has taken hold in a host.

*Disease:* A term often applied when an infection starts producing symptoms in a host.

*Incidence:* The number of new infections or cases of disease appearing in a population per time unit. Often expressed as a fraction of the total population.

*Prevalence:* The total number of infections or cases of disease existing in a population. Often expressed as a fraction of the total population.

With this terminology in mind, let us put the  $I$  model into the form of prevalence, as a fraction of the entire population. In this case, prevalence is just  $p = I/N$ . Start where we left off, with

$$\frac{1}{I} \frac{dI}{dt} = \beta \left( 1 - \frac{I}{N} \right) - \alpha$$

multiply through by  $I$ ,

$$\frac{dI}{dt} = \beta I \left( 1 - \frac{I}{N} \right) - \alpha I$$

divide through by  $N$ ,

$$\frac{d \frac{I}{N}}{dt} = \beta \frac{I}{N} \left( 1 - \frac{I}{N} \right) - \alpha \frac{I}{N}$$

substitute prevalence  $p = I/N$ ,

$$\frac{dp}{dt} = \beta p (1 - p) - \alpha p$$

and, finally, divide through by  $p$ ,

$$\frac{1}{p} \frac{dp}{dt} = \beta (1 - p) - \alpha$$

Now think about the term  $(1 - p)$ . This “one minus the prevalence” represents the fraction of the population that is susceptible to the disease. But some fraction of the population may have natural immunity to the disease, and another may have been successfully vaccinated against the disease. Let us call this fraction  $v$  and subtract it too from the fraction that is susceptible, finally giving

$$\frac{1}{p} \frac{dp}{dt} = \beta (1 - v - p) - \alpha \quad (15.3)$$

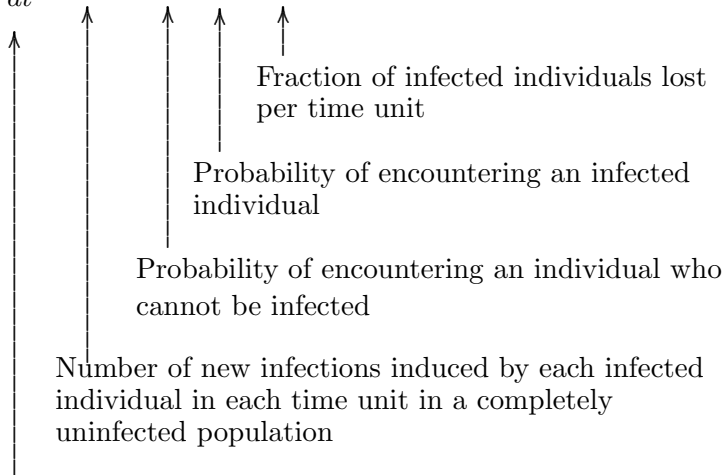
Whew, that is the final *I* model—the starting place for analysis!

You will see in an upcoming chapter that Equation 15.3 is identical to a model of habitat destruction in which plants are isomorphic to “infections” of the landscape, and that habitat destruction, which “protects” the landscape from infection by plants, is isomorphic to vaccination.



Here is the equation with term-by-term explanations:

$$\frac{1}{p} \frac{dp}{dt} = \beta (1 - v - p) - \alpha \quad (15.3)$$



Relative growth in prevalence under conditions prevailing at time  $t$

Keep in mind that this is a constant-population approximation. Whenever an individual dies of the disease, a new susceptible individual enters the population.

## 15.6 Analysis of the I model

With  $v$  as the prevalence of vaccination in a population, what will the I model reveal about vaccination? In an uninfected population the prevalence of infection will be zero ( $p=0$ ), so the number of new infections produced per infected individual per time unit will be  $\beta(1-v)$ .

On average, a fraction  $\alpha$  will die per time unit, so the average duration of infection will be  $1/\alpha$ , assuming complete randomness. If  $1/10$  die per year, for example, the average duration of infection will be 10 years.

This makes  $R_0(v) = \beta(1-v) \times (1/\alpha) = (\beta/\alpha)(1-v)$ . And the disease will decline to extinction if  $R_0(v) < 1$ —that is, if  $R_0(v) = (\beta/\alpha)(1-v) < 1$ , which you can work out algebraically in a few steps to  $v > 1 - \alpha/\beta$ .

Look what this means. A disease that infects 4 individuals per year in a totally uninfected population ( $\beta = 4$ ), and which remains infectious for one year ( $1/\alpha = 1$ ), will decline to extinction if  $v > 1 - 1/4 = 3/4$ . If only slightly more than  $3/4$  of the population is vaccinated, that disease will eventually vanish. Remarkably, a disease can be eradicated even if the whole population cannot be vaccinated! Largely because of this, society can develop programs striving toward the conquest of disease.

What does the  $I$  model reveal about the evolution of infectious disease? The pathogen has many more generations and can therefore evolve biologically more rapidly than the host, and  $\alpha$  and  $\beta$  can evolve to benefit the pathogen.

Because  $\beta$  enters the equation with a plus sign and  $\alpha$  enters with a minus sign, the disease will spread more rapidly— $(1/p)(dp/dt)$  will be larger—if  $\beta$  increases and  $\alpha$  decreases.

This means that, genetics permitting, a successful disease operating according to this or any similar model will tend to become *more infectious* (higher  $\beta$ ) and *less virulent* (lower  $\alpha$ ) over time. At the limit, nearly everybody will be infected but the effect on anybody will be minimal. Polio in humans before the 20th century, and SIV in monkeys, are examples.

In the ultimate limit, a disease could evolve to negative virulence—that is, to be a mutualism with the host. Rhizobial bacterial in legumes may be an example.

As usual, there are refinements to this idea, in part because infectivity and virulence are not independent. Diseases that evolve to be more infectious may have to use more of their victims' metabolic resources, and consequently may become more virulent in the process. Again, such refinements can be addressed in more specific models.

## 15.7 The rsN model again

Let's return to shorter time frames without evolution. Notice that prevalence  $p$  changes with time as the epidemic spreads, but  $\beta$ ,  $\alpha$ , and  $v$  remain constant. So starting with

$$\frac{1}{p} \frac{dp}{dt} = \beta(1 - v - p) - \alpha$$

rearranging terms,

$$\frac{1}{p} \frac{dp}{dt} = (\beta(1 - v) - \alpha) - \beta p$$

and substituting  $r = \beta(1 - v) - \alpha$ ,  $s = -\beta$ , and  $N = p$ ,

$$\frac{1}{N} \frac{dN}{dt} = r + sN$$

Voilà, the epidemiological  $I$  model is revealed to be just the standard model of ecology in another disguise! But now, with mechanisms included (infectivity, virulence, vaccination), deeper conclusions can be reached.

In getting to this standard model, for example, we set  $s$  equal to  $-\beta$ . Because  $\beta$  is positive, the density dependence term  $s$  is negative. Negative  $s$  implies logistic growth (positive  $s$  is orthologistic), meaning that  $N$  will reach a carrying capacity—an equilibrium, a steady state. But to arrive at the standard model, we set  $N$  equal to  $p$ , so since  $N$  reaches an equilibrium in the standard model, the prevalence  $p$  will reach an equilibrium in the  $I$  model.

Without further analysis you can therefore conclude that a disease will not necessarily infect an entire population, but that its prevalence will level out when it reaches a carrying

capacity, at the equivalent of  $-r/s$ . Substitute backwards ( $r = \beta(1-v) - \alpha$  and  $s = -\beta$ ) and you will find the carrying capacity of the disease:

$$\hat{p} = 1 - \frac{\alpha}{\beta} - v \quad (15.4)$$

The small hat atop the  $p$  is just a reminder that this is not the variable prevalence  $p$ , but rather the fixed value of the equilibrium prevalence,  $\hat{p}$ .

Think about the approach on Page 225, which used  $R_0$ . Here is another way to get the result. Since  $v$ , the proportion of the population vaccinated, appears in the equation with a minus sign, that means that the greater the proportion vaccinated, the lower the equilibrium prevalence  $\hat{p}$ . In fact, setting  $\hat{p} = 0$  and solving for  $v$ , when  $v = 1 - \alpha/\beta$ , the prevalence  $p$  will be zero and the disease will be eradicated. (Actually, for a margin of error, when  $v \geq 1 - \alpha/\beta$ ).

## 15.8 Application to an actual outbreak

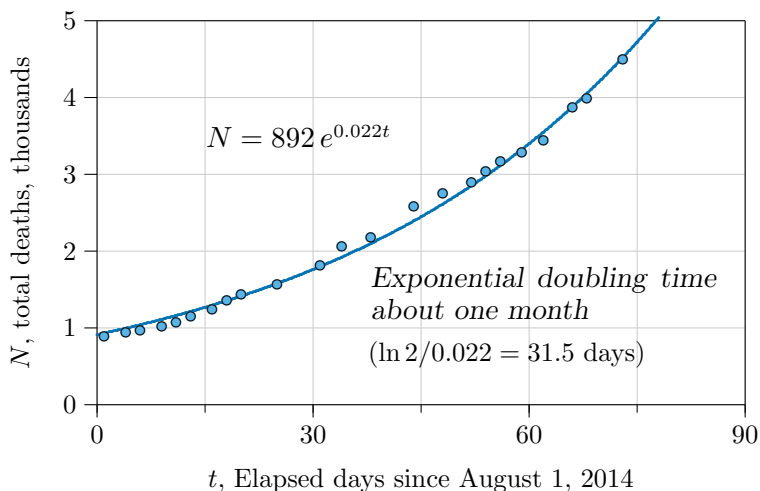
An ominous outbreak of Ebola★ in West Africa became widely known in 2014, with the rate of deaths repeatedly doubling and redoubling. By the fall of that year cases started appearing on other continents.

Ebola apparently enters human populations from wild animals such as bats, in whom it is not particularly virulent. It has not, however, adapted to the human body (Figure 14.5, right). It becomes such a dread disease in humans because it exploits almost all of the body's exit portals (Table 14.1)—not simply by finding limited passages through them, but by

completely destroying them. Some diseases may induce vomiting or diarrhea, for example, as a means of for the pathogen to exit the alimentary canal, but with Ebola, entire tissue systems are destroyed and chunks of intestine accompany the exit.

At the time of the outbreak, two of us (CL, SW) were jointly teaching courses in the United States in quantitative ecology and in the ecology of disease, using tools illustrated thus far in this book. A level of fear prevailed in the country because the disease had just reached the U.S., with a few deaths in U.S. hospitals. Along with our students, we decided to make Ebola a case study for application of the disease equations, applying the principles week-by-week as the outbreak was advancing. Hundreds of thousands of deaths had been predicted by health organizations. This section describes what we did and what we discovered.

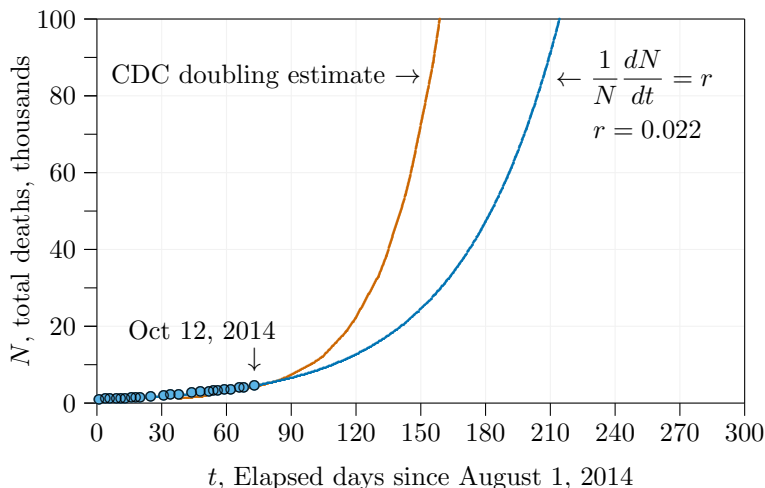
**Real-time data.** Data from the World Health Organization (WHO★) and other official sources had been tabulated on a website about Ebola in West Africa,★ and you can select a date there to see exactly which data were available when we started tracking the outbreak, or at any subsequent time. The site listed both the number of individuals infected with Ebola and the number who had died, but in the early days of the outbreak we guessed that the number of deaths would be more reliable. Moreover, the world was paying greatest attention to deaths, so we hypothesized that these numbers would most strongly influence social efforts to combat the disease.



**Figure 15.2.** *Ebola deaths reported at the time Ebola began to appear outside of Africa.*

We thus started with total deaths, plotting them as in Figure 15.2. The number of deaths was not only increasing but accelerating, seemingly on an exponential course. The calculated doubling time (Equation 5.4) was 31.5 days, not quite what U.S. Centers for Disease Control (CDC★) had found earlier, but within reasonable correspondence. They estimated 15–20 days to double in one country and 30–40 in another (Meltzer et al., 2014).

Calculating from these doubling times and extending for several more months results in the number of deaths shown in Figure 15.3. Before five months with the estimates we made during class (blue curve in the figure) and before three



**Figure 15.3.** *Ebola deaths extended according to doubling times seen early in the outbreak.*

months with the earlier estimates (red curve), the number of deaths was predicted to exceed 100,000.

But there is a flaw in this approach. As shown by the calculations on bacteria (page 25) and Darwin's calculations on elephants (page 27), exponential growth models cannot be extended very far. They can be quite accurate a limited number of time units in the future. But when applied to biological populations both exponential and orthologistic models inevitably fail when extended indefinitely. Actually, one view is that they do not really fail—they just warn that



*Ebola deaths.*  
**Table 15.1.** *Consequences of unlimited doubling in*

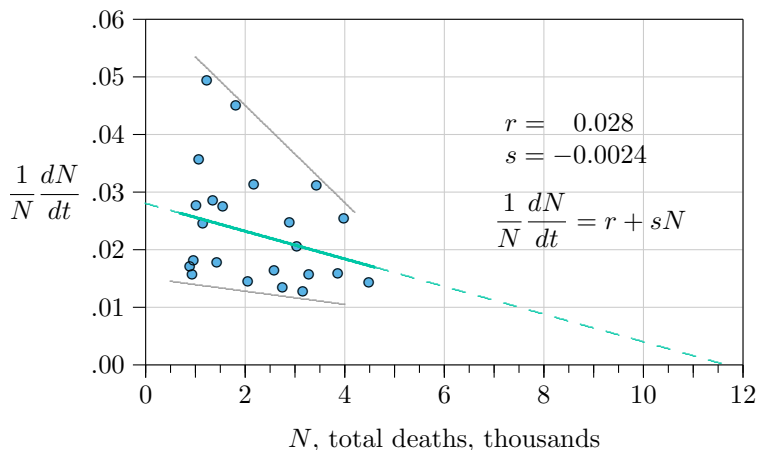
Days	Years	Total Deaths
0	0.00	892
100	0.27	8,412
200	0.55	79,335
300	0.82	748,267
400	1.10	7,057,440
500	1.37	66,563,800
600	1.64	627,811,000
700	1.92	5,921,330,000
710	1.94	7,411,030,000

some other growth model will supplant them before populations grow too large.

In fact, assuming the unrestrained doublings of exponential growth is tantamount to assuming a disease will kill the entire world, with the only question being when. Table 15.1 shows the results of doubling at the rate illustrated by the blue curve in Figure 15.3, extended farther. At this rate the entire human population would be extinguished in less than two years!

**Expected moderation.** Of course, the entire human population will not be extinguished by a manageable disease. Draconian measures would be put in place long before—isolating those infected, closing borders, and more. In effect, the growth rate  $r$  will be moderated by strong negative social pressure, term  $s$ .

When would such negative pressure appear in the data? Could it be seen early in the Ebola outbreak, when we and the students began watching? Because the basic disease equation



**Figure 15.4.** The data of Figure 15.2 converted to individual change in death rate as a function of number of deaths.

is equivalent to the  $rsN$  model (page 227), we thought early trends might appear if we examined the data in terms of  $r$  and  $s$ . The individual growth rate in deaths,  $(1/N) dN/dt$ , could be examined and plotted against the total number of deaths,  $N$ . This is Figure 15.4, with the same data as Figure 15.2, just reformulated.

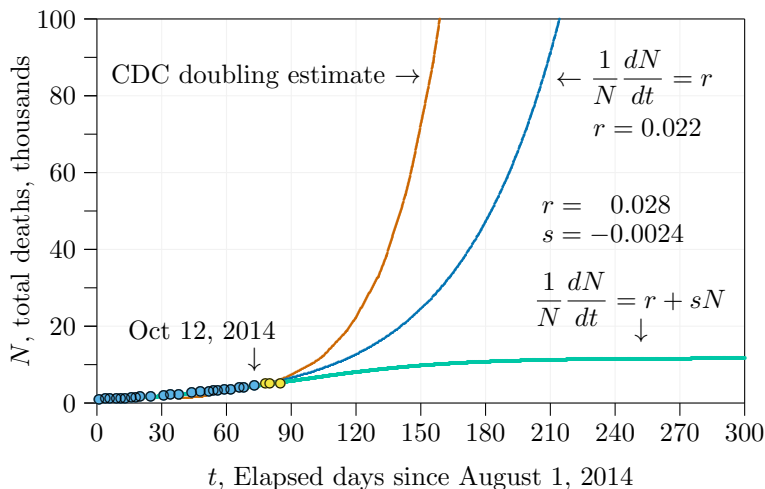
The data show quite a bit of noise, but with a clear downward trend, with the rate in the total number of new deaths decreasing as deaths increase. Both the upper and lower ranges of points are decreasing (gray lines). The green line through the averages (least-square regression line, solid, with  $r$  and  $s$  as shown in the figure) projects forward (dashed) to about 12,000 deaths before the outbreak would be over—an

extensive human tragedy, but far below the straightforward projections of Figure 15.3.

If this decline in death rate was real, it was likely developing from more and more attention to moderating the disease—medical workers expanding hospitals, populations practicing more careful burials, governments cautioning only justified travel, and the like. When we made the projection of 12,000 in the fall of 2014, we had no certainty about what would happen; we were simply looking at the data, which showed not unrestrained exponential growth, but moderating growth instead.

The next step was to plug the  $r$  and  $s$  derived from the fitted curve into Equation 5.2 and project forward six months or a year. This projection is shown in Figure 15.5. The green curve is the projection from  $r = 0.028$  and  $s = -0.0024$ . It is markedly different than the other two curves, leveling off early and reaching about 12,000 deaths. Also in the figure are three additional points of actual data, in yellow, not sufficiently advanced to tell which of the three curves—red, green, or blue—will be the real one.

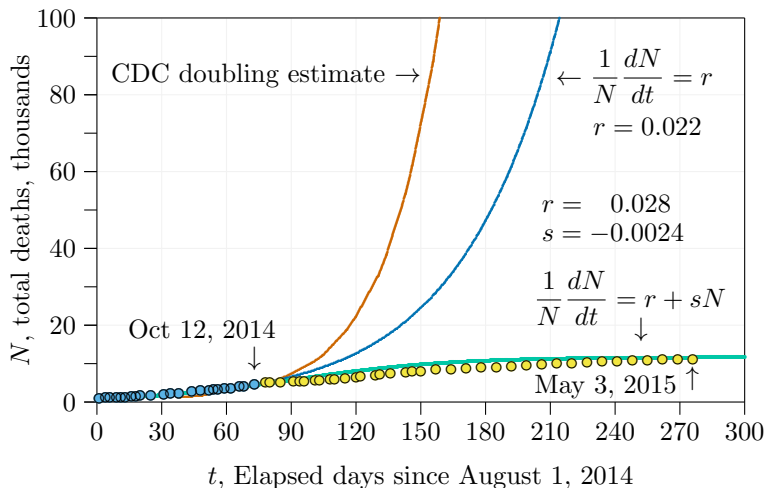
In only a few weeks, however, it became apparent that the  $r + sN$  curve was the most accurate. By the end of the winter semester (about day 140 in the graphs) it was clear that the outbreak was coming under control, and that the number of deaths was fairly close to our initial projection. After tracking the outbreak with our students through the winter and spring semesters, we could see how remarkable that early projection was (Figure 15.6). Reading the data



**Figure 15.5.** Ebola deaths projected by Equation 5.2 using the parameters of Figure 15.4.

carefully early in the crisis gave an accurate projection of the outcome, from a simple model indeed!

**Doubling times.** This example provides a good place for us to reconsider doubling times (Equation 5.4), introduced with exponential growth on page 52. Recall that exponential growth is the infinitely thin dividing line between logistic and orthologistic growth, and has the property of a fixed “doubling time.” In other words, there is a specific time interval—call it tau ( $\tau$ )—during which the population exactly doubles. In logistic growth the doubling time constantly decreases, while in orthologistic growth it constantly



**Figure 15.6.** Actual development of the outbreak (yellow dots), falling along the projection from October, 2014 (green curve).

increases. On page 53 the doubling time is shown to be the natural logarithm of 2 divided by  $r$ — $(\ln 2)/r$ , or approximately  $0.693/r$ . This is in years if  $r$  is measured per year, days if per day, and so forth.

Thus the doubling time for the exponential curve of Figure 15.2, with  $r = 0.022$ , is  $0.693/0.022 = 31.5$  days. The logistic growth of Figure 15.4 has no fixed doubling time. However, at all times there will be an “instantaneous doubling time,” which will hold approximately for a short time. In particular, near the very beginning of the outbreak—when  $N$  is close to 0—the growth rate is  $r + sN = r + s \cdot 0 = r$ . For the Ebola data early in the outbreak, we found  $r = 0.028$

and  $s = 0.0024$ . The Ebola doubling time, averaged over the countries in which it spread, therefore started out at  $0.693/r = 0.693/0.028 = 25$  days. This is in accord with early estimates made by health organizations.

When we began following the outbreak, about 4.5 thousand deaths had occurred, meaning that the growth rate was  $r+sN = 0.028 - 0.0024 \cdot 4.5 = 0.0172$ , and the doubling time was  $0.693/0.0172 = 40$  days.

The doubling time continued to decrease until the outbreak was conquered and all deaths from Ebola ceased.

**Caveats and considerations.** There was some fortuity in the timing of our initial projection. Shortly after we started the death rate dropped, possibly from increased efforts following intense world-wide attention. Had we made the projection a few weeks later we would have seen two slopes and would have had to guess which would prevail. It turns out that the first slope prevailed, returning about 40 days after our initial projection. But we had no way to know this from the data at the time.

Our approach could also be criticized because the  $r+sN$  equation we used is a hybrid—a single equation trying to represent two different things, in this case infections and deaths. It is reasonable here to base the amelioration parameter  $s$  on the total number of deaths, since deaths were the parameter of world concern. Deaths influence social attention to the disease and efforts to control it. However, what sense is there in saying that deaths grow at rate  $r$ , based on the total number of deaths thus far? Ebola can be transmitted to others shortly after death, but in general deaths do not

cause new deaths. Infections cause new infections, which in turn cause new deaths. If  $N$  represents total deaths, it seems the equations should also have an  $I$  to represent infections, and some fraction of infections should result in deaths—as in this two-dimensional system of equations.

$$\begin{aligned}\frac{dI}{dt} &= \beta I - \gamma I - \alpha I - s N I \\ \frac{dN}{dt} &= \alpha I\end{aligned}\tag{15.5}$$

The two dimensions are  $I$ , the number of existing infections, and  $N$ , the cumulative number of deaths. Infectivity is  $\beta$ , the rate of recovery from infection is  $\gamma$ , and the rate of death from the disease is  $\alpha$ . These correspond to the notation in Figure 15.1. In addition, the term  $sN$  moderates the growth of the infection by representing all the cautions and infrastructure put in place against the disease as the number of deaths increased.

No factor like  $1 - v - p$ , representing the fraction of susceptible individuals as in Equation 15.3, is needed to multiply the  $\beta$  term here, because both in the early stage and at the outbreak the prevalence was low and there was no vaccine, so almost everyone was susceptible. And with this rapidly progressing disease the population remained almost constant, so births could be considered negligible. Equation 15.5 is thus still a simplified equation.

As simplified as it is, however, Equation 15.5 carries more parameters than can be perceived in the raw data. The death

rate from the disease  $\alpha$ , the recovery rate  $\gamma$ , the infectivity  $\beta$ , and even the number of infections  $I$ , can only be discovered through the use of special research programs. But even at the beginning of an outbreak, and even for a poorly understood disease, there may be enough data to determine the doubling time for deaths from the disease, and how the doubling time is changing—enough data to determine  $r$  and  $s$ , even if little more.

This is fortunate, because Equation 15.5 can be reduced in dimension and approximated by the  $r+sN$  form. Without the amelioration term  $sNI$ , the two dimensions are independent and growth of each is exponential, with  $N$  being the integral of  $I$ . Because the integral of an exponential is still exponential, the two can be approximated by a single equation of one fewer dimension, with the amelioration term  $sNI$  reinstated. In this way, total deaths become a legitimate surrogate for infections in low-prevalence outbreaks, as in the present example of Ebola.

And as we noted, this gave an accurate projection on the course of a dread disease, from a very simple model indeed!

## 15.9 Conflicting ethics

Fundamental conflicts in ethical behavior are hidden just below the surface of the cold mathematics in these equations, particularly in Equation 15.4. Virulence  $\alpha$  appearing in the numerator of a term with a minus sign means that the greater the virulence, the lower the equilibrium level of disease,  $\hat{p}$ . In the absence of vaccination ( $v = 0$ ), setting  $\hat{p} = 0$  and solving for  $\alpha$  yields  $\alpha = \beta$ . Artificially increasing the virulence  $\alpha$  of



a disease to equal or exceed the infectivity  $\beta$  will therefore drive the disease extinct.

The enduring ethical conflict here is between the individual and the population. With all other things being equal, working to reduce virulence benefits the individual but may cause more individuals in the population to become infected. Working to increase virulence, in contrast, harms individuals but may reduce the number who become infected.

The ethics of modern medicine emphasizes individuals—working to cure disease and reduce virulence, ameliorating symptoms, reducing discomfort, and recognizing patient needs. Increasing the virulence of a disease in a human patient to reduce its spread is unthinkable, both in medicine and public health. The ethics of modern agriculture, however, are the diametric opposite. If a crop is infected with a destructive communicable disease, entire fields of the crop may be mowed, burned, or otherwise disposed of. Infected populations of poultry and livestock are treated similarly, killed en masse and buried or burned to contain the disease.

Artificially altering the infectivity  $\beta$  is also a possibility. In Equation 15.4,  $\beta$  appears in the denominator of a term having a minus sign—meaning that decreasing  $\beta$  will decrease the equilibrium level of the disease,  $\hat{p}$ . Ethical conflicts also arise here, though they are not as stark as the conflicts connected with  $\alpha$ .

During the influenza epidemic of 1918–19, San Francisco leaders required citizens to wear breathing masks—for “conscience, patriotism, and self-protection,” wrote the mayor.



**Figure 15.7.** *Funeral pyre of infected cows. Exterminating a living organism when it is infected artificially increases the virulence of the disease to something like  $\alpha \rightarrow \infty$ .*

This lowered  $\beta$  by containing respiratory droplets from infected individuals, and lowered the chance of infected droplets entering the respiratory systems of susceptible individuals, in turn reducing the infectivity  $\beta$ . Some citizens, however, refused to wear the masks.

During the Ebola outbreak of 2014–15, amidst fears and warnings of the disease becoming established around the world, some U.S. governors ordered temporary quarantine of returning medical workers who had been in direct proximity with Ebola, until it was clear that they were not infected. At least one refused the quarantine based on individual rights, and the courts upheld the refusal.

These ethical conflicts surrounding  $\beta$  are not as grim as those surrounding  $\alpha$ , with options currently practiced for domestic plants and animals but so extreme that they are never proposed for human populations.

It is curious that these high-level social dilemmas are perceptible within the most basic equations of ecology. Science can inform such ethical issues, but society must decide them.



**Figure 15.8.** *The slogan “Obey the laws and wear the gauze” accompanied regulations intended to protect public and individual health in 1918–19 San Francisco. Thousands of city residents died of influenza, but at a rate lower than that of many other cities. Most of the public complied with the regulations; some who refused were quarantined in jail. Pictured above are police officers in Seattle in 1918.*

## Chapter 16

### Competition

Ecological competition is a potent force driving organic evolution. When Charles Darwin★ reached the Galapagos Islands★ at age 26, he studied an assortment of fifteen similar species that are now called “Darwin’s Finches”★ (Figure 16.2). His observation that various species had different beak structures, specialized for different foods, led him to question the stability of species. Indeed, such “character displacement” is one of several consequences of ecological competition.



**Figure 16.1.** *The Galapagos Archipelago, on the equator more 500 miles off the west coast of South America.*



**Figure 16.2.** Three species of Darwin's finches: Sharp-beaked ground finch, *Geospiza difficilis* (left); cactus ground finch, *G. scandens* (middle); and large ground finch, *G. magnirostris* (right).

Seeing this gradation and diversity of structure in one small, intimately related group of birds, one might really fancy that from an original paucity of birds in this archipelago, one species had been taken and modified for different ends.

—Charles Darwin

## 16.1 The niche concept

A species' niche is the range of environmental factors that allow that species to survive and reproduce. A particular tree species, for example, may be able to live where temperatures do not drop below  $-40^{\circ}$ , and where yearly precipitation is at least 750 mm. Perhaps it also needs open sunlight and an appropriate collection of root fungi.★ Such are the parameters of a niche.

G. Evelyn Hutchinson,★ one of the great ecologists of the twentieth century, envisioned the parameters that form a niche as an “ $n$ -dimensional hyperspace.” The “fundamental niche” is the set of conditions allowing the species to survive

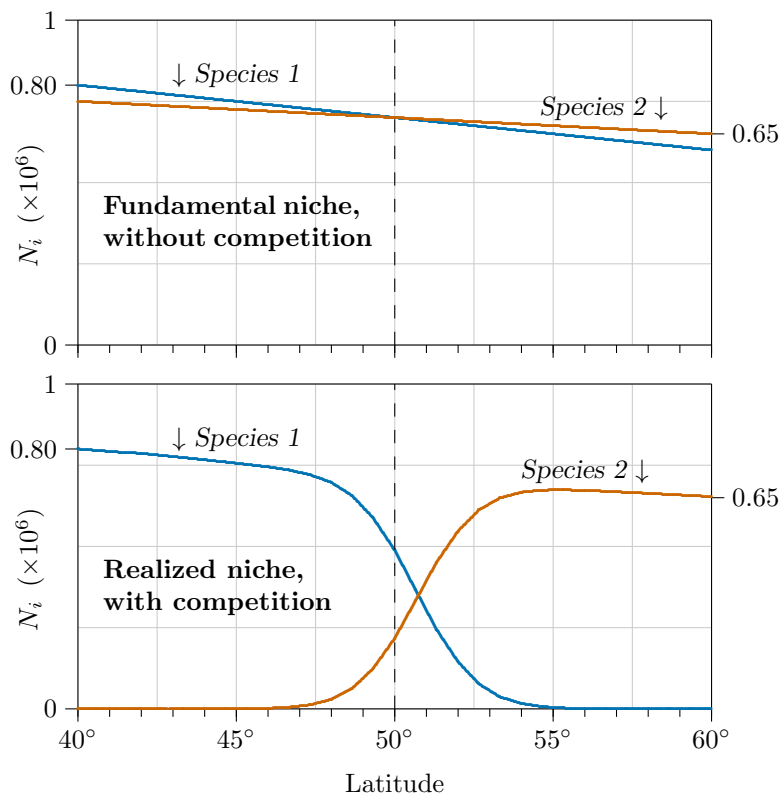
if there are no other species interfering. Physical conditions are chief among those. The “realized niche” is the real life niche—where species are restricted by interactions with other species.

Consider latitude on the earth’s surface, which is connected to several parameters such as sunlight and temperature. And consider two species that can thrive anywhere between  $40^\circ$  and  $60^\circ$  latitude, and whose density drops slowly with increasing latitude (Figure 16.3).

At the top of the figure are two nearly horizontal lines representing the abundance you might observe of the two species as you travel north. If free of Species 2 (its competitor), Species 1 (blue line) declines slowly in abundance in more northerly climates. Species 2 similarly declines in abundance (red line), but compared with Species 1 fares a little better in the north and a little worse in the south.

When these two species are together they compete with each other—each suppressing the other. Using competition equations like those presented in this chapter, we see that in the south, where Species 1 fares better, it takes over and dominates. In the north, in contrast, where Species 2 fares better, it dominates instead (Figure 16.3, bottom).

You see that there can be a sharp change in abundance even with only very slight changes in species characteristics. A range of one species can end and that of a new species can begin, even though you may not be able to discover anything from either species alone as to why they switch their dominance. And the switch-over point need not correspond to the exact place in which their dominance switches. Here the



**Figure 16.3.** Species living apart along a spatial gradient (above) and living together along the same gradient (below).



**Figure 16.4.** Zonation on a three-year-old fen, Bluebird Prairie, Upper Midwest.

actual switch-over point is a few degrees to the north because of the migration simulated in the model. This phenomenon is called “competitive exclusion” and, when it occurs over space like this, “zonation.”

Any environmental gradient can induce zonation. Figure 16.4 illustrates this on a restored prairie in the North American Upper Midwest. Though less than ten meters, the variation in elevation is enough to induce a mild moisture gradient. The entire area had been converted from a corn field to a restored prairie and seeded uniformly with a mixture



of prairie grasses and prairie flowers, but distinct boundaries arose only three years after restoration.

All the upland areas, labeled 1, contained standard restored prairie flora such as *Andropogon gerardi*★ (Big Blue-stem grass) and rapidly emerging flowers such as *Rudbeckia hirta*★ (Black-eyed Susan). But in successive zones surrounding mild depressions in the landscape, labeled 2 to 4, there were sharp transitions to moisture-loving genera such as *Typha latifolia*★ (cattail) and *Stachys palustris*★ (Smartweed).

*Fundamental niche*: The conditions under which a species can live, absent interference from other species.

*Realized niche*: The conditions to which a species is restricted by interactions with other species.

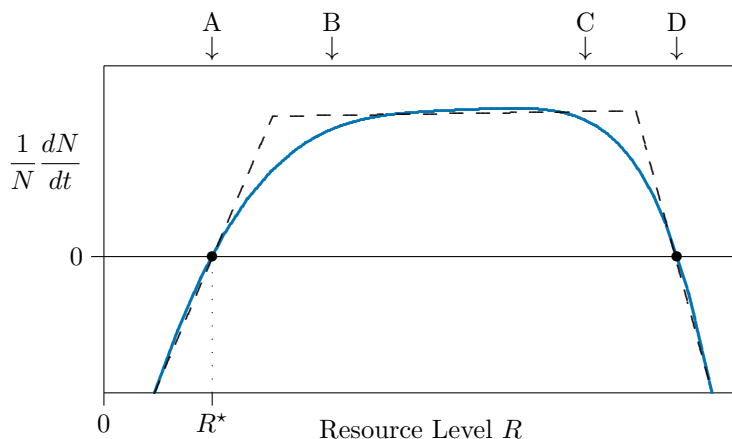
## 16.2 Resource competition

Competition among two species occurs when the interaction terms  $s_{1,2}$  and  $s_{2,1}$  in Equation 8.1 are both negative. This rather abstract approach does lead to broad insights, but for other kinds of insights let us proceed to a more *mechanistic* view. Instead of abstract coefficients representing inhibition among species, let us consider *resources* which species need to thrive and survive. The species will not interact directly—they never even need to come into contact—but will influence each other through their use of a common resource, which they both need for maintenance and growth of their populations.

Resource competition is one of the oldest parts of ecological theory, introduced in the late 1920s by mathematician Vivo Volterra.★ We will start where he started, considering what have been called “abiotic resources”.

Species require sunlight, space, nitrogen, phosphorous, and other resources in various amounts. If a resource is too rare, populations cannot grow, and in fact will decline. In Figure 16.5 this is shown in the region to the left of the arrow marked A, in which the individual growth rate  $1/N dN/dt$  is negative.

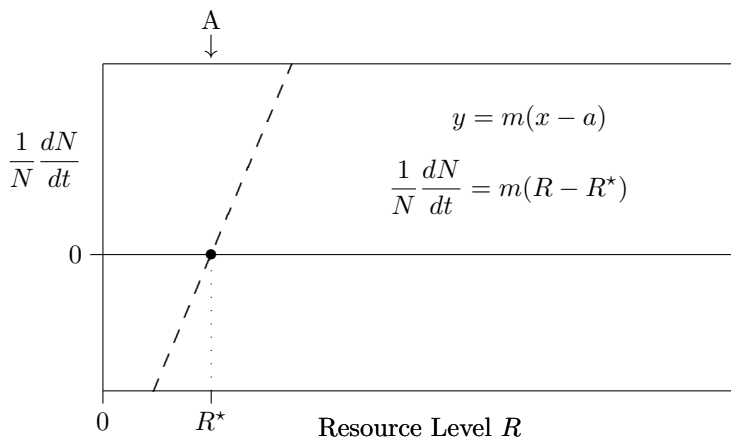
At higher resource levels the growth rate increases and, at point A, the population can just barely maintain itself. Here the individual growth rate  $1/N dN/dt$  is zero. This level of resources is called  $R^*$ , pronounced “are star”. At higher levels of resource, above  $R^*$ , the population grows because  $1/N dN/dt$  becomes positive.



**Figure 16.5.** Growth curve generalized for any resource, with a piece-wise linear approximation sketched as dashed lines.

Once resources are abundant—approximately above B in the figure—needs are satiated and the addition of more resources does not make any large difference. Population growth stays approximately the same between marks B and C.

At very high levels, too much resource can actually harm the population. Too much sunlight can burn leaves, for example, while too much nitrogen can damage roots. At this point, above C in Figure 16.5, the growth rate starts falling. By D the species can again just barely hold its own, and to



**Figure 16.6.** Growth curve with only the left linear piece of Figure 16.5, usable because species tend to keep resources low.

the right of D the species is killed by an overabundance of resources.

Such high resource levels, however, are not usually observed, because species draw resources concentrations down by using them up. Unless extreme environments are being modelled, only the left dashed linear piece of Figure 16.5 needs to be modelled, as shown in Figure 16.6.

At this point, it is helpful to review various forms for the equation of a straight line. The usual slope–intercept form— $y = mx + b$ , which is a  $y$ -intercept form—is not as useful here. It’s the  $x$ -intercept form,  $y = m(x - a)$ , that comes into play

for writing a mechanistic resource model for single species population growth.

1. *Slope-intercept form:*  $y = mx + b$   
(slope  $m$ ,  $y$ -intercept  $b$ )
2. *Intercept-intercept form:*  $y = b(1 - x/a)$   
( $x$ -intercept  $a$ ,  $y$ -intercept  $b$ )  
( $m = -b/a$ )
3. *Slope- $x$ -intercept form:*  $y = m(x - a)$   
(slope  $m$ ,  $x$ -intercept  $a$ )  
( $b = -m/a$ )

The zero-growth point,  $R^*$ , is important in the theory of resource competition. It is the amount of resource that just barely sustains the species. If the resource level is less than  $R^*$ , the species dies out; if it is greater, the species grows and expands. The resource level in the environment therefore is expected to be at or near the  $R^*$  value of the dominant species. If it is above that level, the population grows, new individuals use more resource, and the resource level is consequently reduced until growth stops.

$R^*$  can be measured in the greenhouse or the field. In the greenhouse, for example, you might arrange plants in 20 pots and give them different amounts of nitrogen fertilizer in sterile, nutrient-free soil. In the complete absence of fertilizer,

the plants will die. With larger amounts of fertilizer the plants will be luxuriant, and when there is too much fertilizer, the resource will become toxic, again leading to dieback in the plants. You can thus measure the curve of Figure 16.5 fairly easily and find the point on the left where the plants just survive. This is their  $R^*$ .

You can also measure this value for different species independently, and from the results estimate how plants will fare living together. To start, suppose that one resource is the most limiting. Represent the amount of that limiting resource available in the environment at time  $t$  by the symbol  $R(t)$  or, for shorthand, simply  $R$ . The amount in excess of minimal needs is  $R - R^*$ , and that amount of excess will determine the rate of growth. A tiny excess will mean slow growth, but a larger excess can support faster growth. So the equation in Figure 16.6 shows the individual growth rate,  $1/N dN/dt$ , being proportional to how much resource exists in excess.

As before,  $N$  measures the size of the population at time  $t$ , in number of individuals, total biomass, or whatever units are relevant to the species being studied.  $R^*$  is the smallest amount of resource that can support a viable population, and  $m$  tells how the individual growth rate,  $(1/N) dN/dt$ , depends on the amount of resource available in excess of minimal needs.

Now let us say that  $R_{\max}$  is the maximum amount of resource available in the environment, in absence of any organisms, and  $u$  is the amount of resource used by each living

organism in the population. Then  $uN$  is the amount of resource tied up in the population at time  $t$ .  $R_{\max} - uN = R$  is the amount of resource *not* used by the population. This is the basis of a resource theory that assumes resources are released immediately upon death of an organism, and it has many of the important properties of more complex resource models.

Start with the above statements in algebraic form,

$$\frac{1}{N} \frac{dN}{dt} = m(R - R^*) \quad \text{and} \quad R = R_{\max} - uN \quad (16.1)$$

then substitute the equation on the right above into the one on the left. This gives

$$\frac{1}{N} \frac{dN}{dt} = m \left( \underbrace{R_{\max} - uN}_R - R^* \right)$$

Multiplying through on the right by  $m$  and rearranging terms gives

$$\frac{1}{N} \frac{dN}{dt} = m(R_{\max} - R^*) - umN \quad (16.2)$$

Notice that the first term on the right is a constant and the second term is a constant times  $N$ . Does this look familiar? This is just density-regulated population growth in disguise—the  $r + sN$  model again!

$$\frac{1}{N} \frac{dN}{dt} = r + sN, \quad r = m(R_{\max} - R^*), \quad s = -um$$

Recall that this also happened for the epidemiological  $I$  model. And it will arise occur again in future models.

## 16.3 Competitive exclusion

Consider what will happen with two species using the same resource, such as light or space or nitrogen fertilizer. The amount of resource available will be the maximum amount,  $R_{\max}$ , minus what is tied up in all individuals of all species. With  $u_i$  being the amount of resource tied up in each individual of species  $i$ , the resource remaining at any time will be

$$R = R_{\max} - u_1 N_1 - u_2 N_2$$

Or for many species

$$R = R_{\max} - u_1 N_1 - u_2 N_2 - u_3 N_3 - \cdots - u_h N_h$$

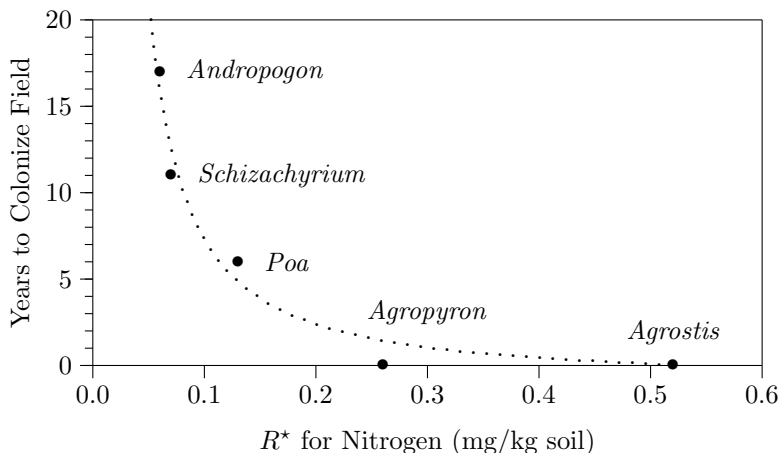
$$R = R_{\max} - \sum_{i=1}^h u_i N_i \quad (16.3)$$

Each species has its own growth equation, identical in form for all species, but different in the critical level of resource,  $R_i^*$ , and the growth coefficient,  $m_i$ :

$$\frac{1}{N_i} \frac{dN_i}{dt} = m_i (R - R_i^*) \quad (16.4)$$

What remains is to consider how the growth coefficient  $m_i$  relates to the minimal level of resource tolerated,  $R_i^*$ . It turns out to be a tradeoff between the two. Consider, for example, a plant species that is limited by the amount of nitrogen available, as plants are. And to have a large growth coefficient  $m_i$  the plant must produce abundant seed. To

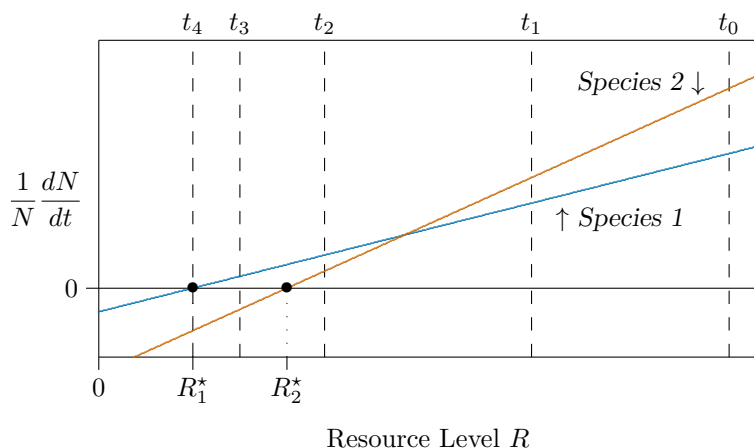




**Figure 16.7.** Tradeoff measured between colonization and ability to exploit nitrogen (Tilman 1994, *Ecology* 75:2–16).

have superior nitrogen use, measured by a low value of  $R^*$ , it needs abundant roots. But it cannot do both. There is a limited amount of solar energy to exploit, so if the plant allocates more to roots there is less to allocate to seeds, and vice versa.

It therefore turns out that species which are good *colonizers*, producing abundant seed, are poorer *competitors* for resources, having a higher value of  $R^*$ . This idea is illustrated by measurements reported in Figure 16.7.



**Figure 16.8.** Two species individual growth rate versus resource level, whose time-course is illustrated in Figure 16.9.

In Figure 16.8, tradeoffs are formulated for modelling. Species 2 grows more rapidly when resources are abundant. This is the case at time 0, marked with  $t_0$  on the top axis.

As the populations grow they reduce the amount of resource available in the environment. At time 1, marked with  $t_1$  on the upper axis, Species 2 can continue to grow faster than Species 1, though the margin is deteriorating. But there comes a point at which the resources become depleted enough that the characteristics of Species 2 do not let it gather enough resources to maintain its advantage. This is the crossing point of the blue and red lines in the figure. At

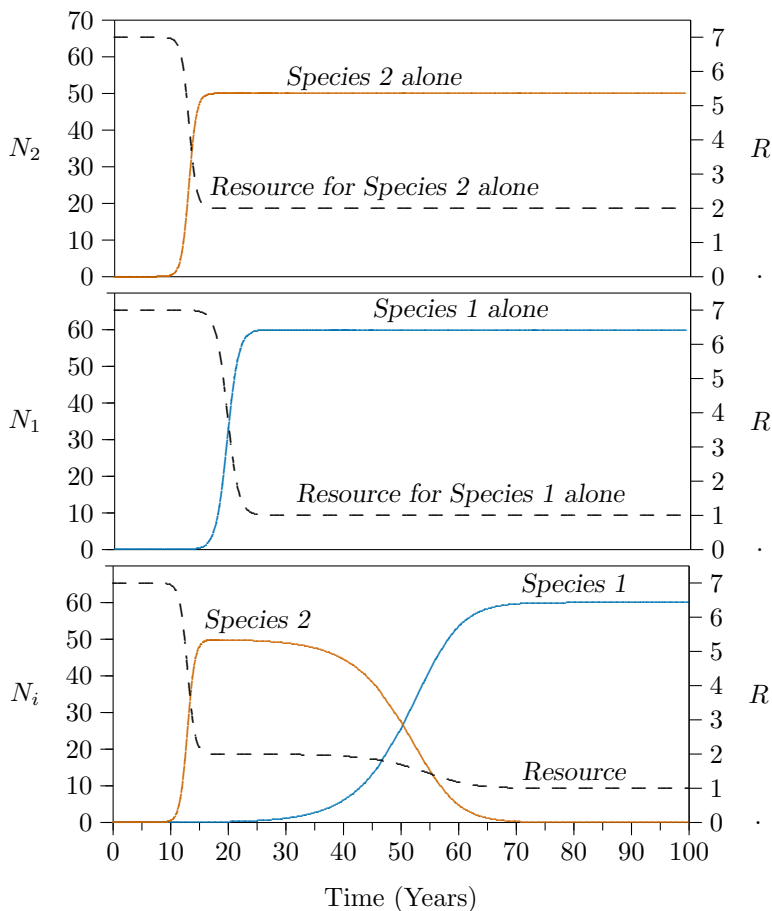
time 2, both species are still growing, but Species 1 is growing faster. At time 3, with still lower resource levels—drawn down by Species 1—the resource falls below the minimal level for Species 2,  $R_2^*$ . The growth rate of Species 2 falls negative and Species 2 starts to die out.

Finally, at time 4, Species 1 depletes the resource to the level that it can just barely survive, and it stands alone, having wiped out its competitor. This process is called “competitive exclusion.”

**H**ow this plays out over time is illustrated in Figure 16.9. At the top, Species 2 alone does just fine, rapidly rising to its carrying capacity of 50 and pulling the resource down to its  $R^*$  of 2. In the middle, Species 1 alone also does just fine, rapidly rising to its carrying capacity of 60 and pulling the resource down to its  $R^*$  of 1.

But grown together, Species 2 makes an initial splash and then declines. This is due to the incessant growth of Species 1, which outcompetes it. Species 1 simply draws the resource down below the level at which Species 2 can survive.

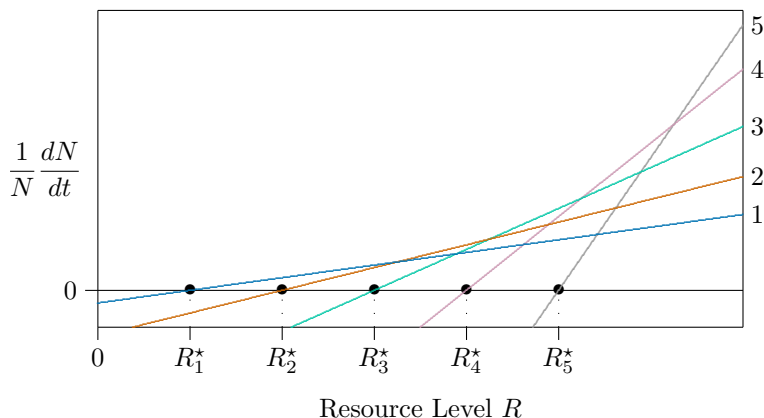
Competitive exclusion, which assumed that no more species could exist than there were resources, was treated as an inviolable law of ecology for over fifty years. In the 1970s, however, this was shown not to be the case (Armstrong and McGehee 1980). More about that later in the chapter.



**Figure 16.9.** Competitive exclusion based on the tradeoffs of Figure 16.8.

## 16.4 Succession

A similar process for more than two species results in a succession of species taking over, one after the other, in an ecological process known as “succession.”



**Figure 16.10.** Multi-species individual growth rate versus resource level, whose time-course is illustrated in Figure 16.11.

In natural systems many species compete, with tradeoffs between their  $R^*$  values and their growth rates, as in Figure 16.10. The following is a program to simulate the differential equations for five species competing for the same resource and producing the curves of Figure 16.11. With only two species, this same program can produce the curves of Figure 16.9.

```

# SIMULATE ONE YEAR
#
# This routine simulates competition differential equations through
# one time unit, such as one year, taking very small time steps
# along the way. Accuracy should be checked by reducing the size of
# small time steps until the results do not significantly change.
# This routine implements <Q>Euler's Method</Q> for solving differential
# equations, which always works if the time step is small enough.
#
# ENTRY: 'N1' to 'N5' are the starting populations for species 1-5.
# 'm1' to 'm5' specify the sensitivity of the corresponding
# species to the available amount of resource.
# 'u1' to 'u5' specify the resource tied up in each species.
# 'R1star' to 'R5star' are the minimum resource levels.
# 'Rmax' is the greatest amount of resource possible.
# 'dt' is the duration of each small time step to be taken
# throughout the year or other time unit.
#
# EXIT: 'N1' to 'N5' are the estimated populations of species 1-5
# at the end of the time unit.
# 'R' is the estimated resource level at the end of the time
# step.

Rmax=R=7;
R1star=1.0; R2star=2.0; R3star=3.0; R4star=4.0; R5star=5.0;
N1=0.000001; N2=0.000010; N3=0.000100; N4=0.001000; N5=0.010000;
m1=0.171468; m2=0.308642; m3=0.555556; m4=1.000000; m5=1.800000;
u1=0.001000; u2=0.001000; u3=0.001000; u4=0.001000; u5=0.001000;

# SIMULATE ONE YEAR

SimulateOneYear = function(dt)
{ for(v in 1:(1/dt)) # Advance a small time step.
  { R=Rmax-u1*N1-u2*N2-u3*N3- # Compute resource remaining.
    u4*N4-u5*N5;

    dN1=m1*(R-R1star)*N1*dt; # Estimate the change in the
    dN2=m2*(R-R2star)*N2*dt; # population of each species.
    dN3=m3*(R-R3star)*N3*dt;
    dN4=m4*(R-R4star)*N4*dt;
    dN5=m5*(R-R5star)*N5*dt;

    N1=N1+dN1; N2=N2+dN2; # Add the estimated change to
    N3=N3+dN3; N4=N4+dN4; N5=N5+dN5; } # each population and repeat.

  assign("N1",N1, enviro=.GlobalEnv); # At the end, export the
  assign("N2",N2, enviro=.GlobalEnv); # results and return.
  assign("N3",N3, enviro=.GlobalEnv);
  assign("N4",N4, enviro=.GlobalEnv);
  assign("N5",N5, enviro=.GlobalEnv); }

```

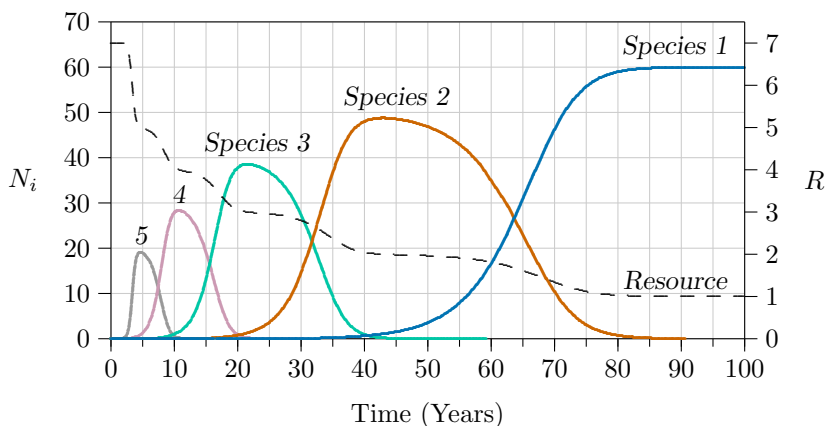
```
# SIMULATE ALL YEARS

for(t in 0:100)
{ print(round(c(t,N1,N2,N3,N4,N5))); # Advance one year.
  SimulateOneYear(1/(365*24)); } # Display results.
                                # Repeat.
```

An environment can change because species living in it have effects that can “feed back” and change the environment itself. In this case the feedback is change in the resource level, which each successive species changes in a way that is compatible with its own existence. There is nothing teleological in this; any species that change the environment in ways not compatible with their own existence simply do not persist, and hence are not observed.

When the program runs, it produces a file excerpted below, which is graphed in Figure 16.11.

t	N1	N2	N3	N4	N5
1	0	0	0	0	0
2	0	0	0	0	13
3	0	0	0	7	391
4	0	0	0	45	1764
5	0	0	1	127	1894
6	0	0	3	329	1743
7	0	0	9	790	1392
:	:	:	:	:	:
60	1649	3536	0	0	0
61	1891	3324	0	0	0
62	2157	3094	0	0	0
63	2445	2846	0	0	0
64	2751	2584	0	0	0
65	3070	2313	0	0	0
66	3397	2039	0	0	0
67	3725	1767	0	0	0
:	:	:	:	:	:
96	5999	1	0	0	0
97	5999	0	0	0	0
98	6000	0	0	0	0
99	6000	0	0	0	0
100	6000	0	0	0	0



**Figure 16.11.** Succession based on the tradeoffs of Figure 16.10.

At the beginning in Figure 16.11, from time 0 to about time 3, the resource is at its maximum level,  $R_{\max}$ , and the abundances of all species are at very low levels. Between times 3 and 5—Species 5, the one with the highest growth rate when resources are abundant—increases rapidly while resources drop accordingly. But near the end of that time the next in the series, Species 4, starts to increase, pulling the resource down below the level that allows Species 5 to survive. Species 5 therefore declines while Species 4 increases. This process continues in succession, with Species 3 replacing 4, 2 replacing 3, and, finally, Species 1 replacing 2. The resource falls in stages as each successive species gains dominance. Finally, when no more superior species exist, the

This process continues in succession, with Species 3 replacing 4, 2 replacing 3, and, finally, Species 1 replacing 2. The resource falls in stages as each successive species gains dominance. Finally, when no more superior species exist, the



system reaches what is called its “climax condition” at about time 90, with resources at a low level.

There is nothing especially remarkable about Species 1. It is simply (1) the best competitor living in the region, meaning better competitors cannot readily arrive on the scene, or (2) the best competitor that evolutionary processes have yet produced. In either case, it is subject to replacement by another—for example, by an “invasive species” arriving by extraordinary means.

Of course, succession in complex natural systems may not be as clear-cut as in our simple models. Multiple resources are involved, species may be very close to each other in their ecological parameters, and stochastic events may intervene to add confusion.



**Figure 16.12.** *Schizacharium* at Cedar Creek with oaks invading.

## 16.5 Single-resource phase space

Some aspects of competition for a resource are clarified by looking at the phase space, as introduced in Chapter 10. Combining Equations 16.3 and 16.4 gives the following as a starting point:

$$\begin{aligned} \frac{1}{N_1} \frac{dN_1}{dt} &= m_1(R_{\max} - R_1^*) - u_1 m_1 N_1 - u_2 m_2 N_2 \\ \frac{1}{N_2} \frac{dN_2}{dt} &= m_2(R_{\max} - R_2^*) - u_2 m_2 N_2 - u_1 m_1 N_1 \end{aligned} \quad (16.5)$$

$\begin{array}{ccc} \uparrow & \uparrow & \uparrow \\ r_i & s_{i,i}N_i & s_{i,j}N_j \end{array}$

As before,  $m_i$  is the rate of growth of Species  $i$  for each level of resource above its minimum resource requirement  $R_i^*$ , and  $u_i$  is the amount of resource tied up in each individual of Species  $i$ . For reference, here is the assignment of parameters in terms of  $r_i$  and  $s_{i,j}$ .

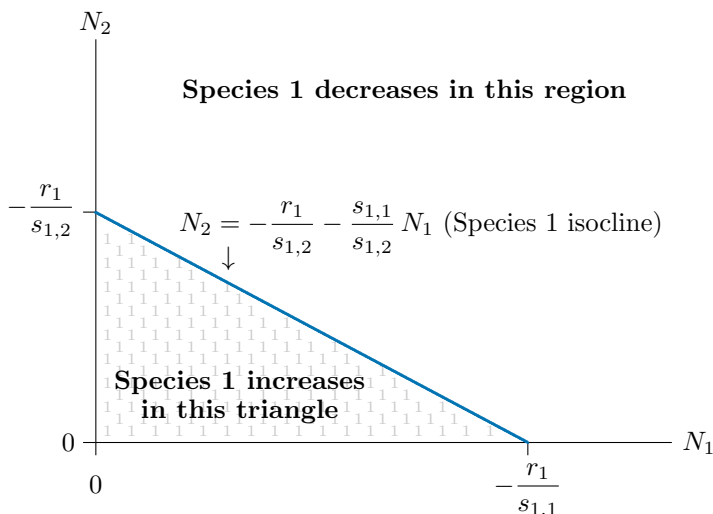
$$\begin{aligned} r_1 &= m_1(R_{\max} - R_1^*), \quad s_{1,1} = -u_1 m_1, \quad s_{1,2} = -u_2 m_2 \\ r_2 &= m_2(R_{\max} - R_2^*), \quad s_{2,1} = -u_1 m_1, \quad s_{2,2} = -u_2 m_2 \end{aligned} \quad (16.6)$$

Where in the phase space will the growth rate be 0 for each species? For Species 1 it will be where

$$\frac{1}{N_1} \frac{dN_1}{dt} = 0 = r_1 + s_{1,1}N_1 + s_{1,2}N_2$$

Solving for  $N_2$  gives

$$N_2 = -\frac{r_1}{s_{1,2}} - \frac{s_{1,1}}{s_{1,2}}N_1 \quad \leftarrow \text{Species 1 isocline} \quad (16.7)$$

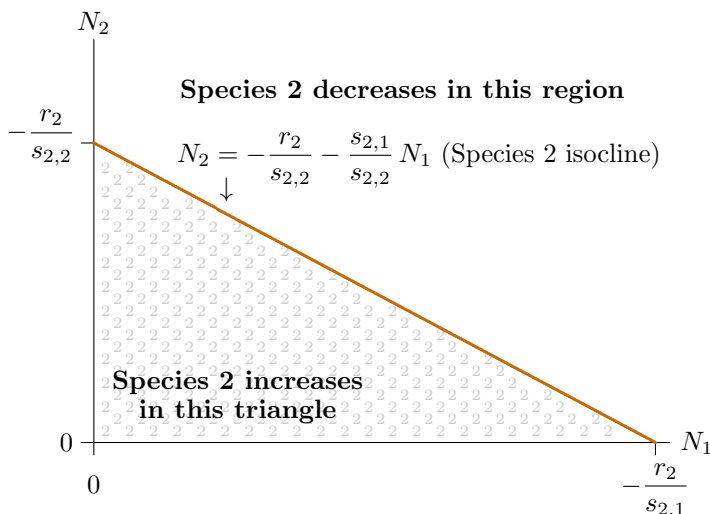


**Figure 16.13.** *Species 1 increases below its isocline, shaded with gray copies of the numeral 1.*

Anywhere along that line, the population of Species 1 will not change, but on either side of the line it will (Figure 16.13). Formulae for the four possible equilibria and their stability are in Table 10.1. The vertical intercept of the isocline, where  $N_1 = 0$ , is  $-r_1/s_{1,2}$ , and the horizontal intercept, where  $N_2 = 0$ , is  $-r_1/s_{1,1}$ . The slope is  $-s_{1,1}/s_{1,2} = (u_1 m_1)/(u_2 m_2)$ .

Similarly, growth of Species 2 will be 0 where

$$\frac{1}{N_2} \frac{dN_2}{dt} = 0 = r_2 + s_{2,2}N_2 + s_{2,1}N_1$$

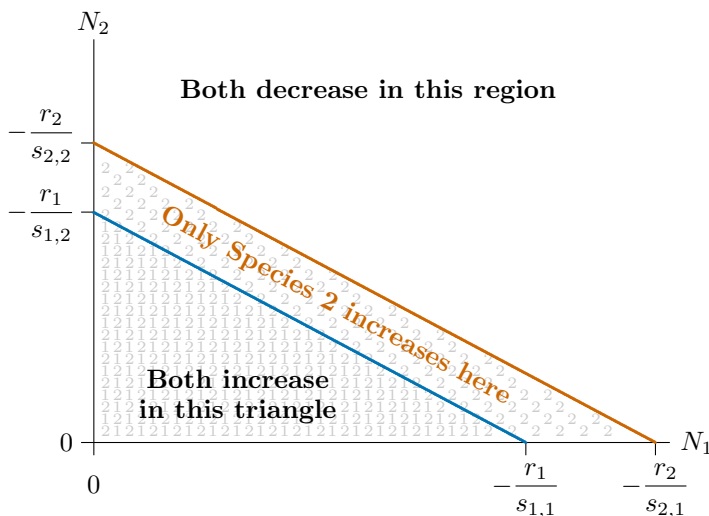


**Figure 16.14.** *Species 2 increases below its isocline, shaded with gray copies of the numeral 2.*

Solving for  $N_2$  gives

$$N_2 = -\frac{r_2}{s_{2,2}} - \frac{s_{2,1}}{s_{2,2}} N_1 \quad \leftarrow \text{Species 2 isocline} \quad (16.8)$$

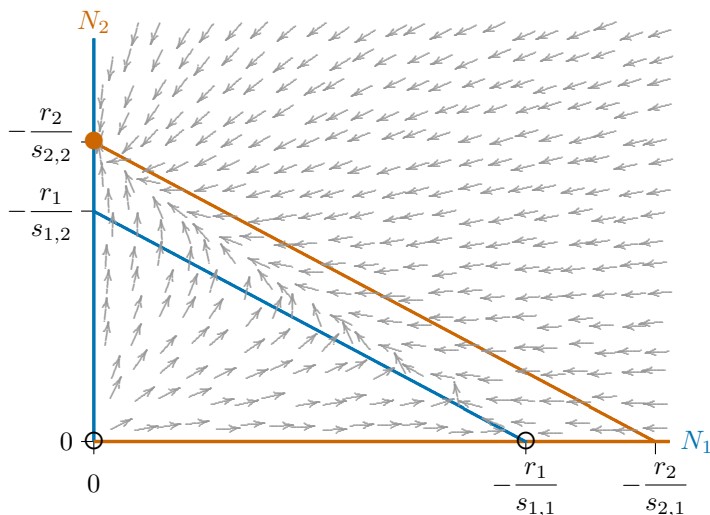
Again, anywhere along that line the population of Species 2 will not change, but on either side of the line it will (Figure 16.14). The vertical intercept of that line, where  $N_1 = 0$ , is  $-r_2/s_{2,2}$ , the horizontal intercept, where  $N_2 = 0$ , is  $-r_2/s_{2,1}$ , and the slope is  $-s_{2,1}/s_{2,2} = (u_1 m_1)/(u_2 m_2)$ .



**Figure 16.15.** Single-species parallel isoclines. Each species increases only below its respective isocline, shaded with gray with the species number, 1 or 2.

Notice this: In terms of the resource, the slope of the isocline for Species 2 is identical to the slope for Species 1—both are equal to  $(u_1 m_1)/(u_2 m_2)$ . What does this mean? It means that the two isoclines are parallel. And that, in turn, means that the two species cannot permanently coexist.

The populations can fall into only one of the three regions of Figure 16.15. If they start in the upper region, they decrease until they enter the middle region. If they start in the lower region, they increase until they also enter the middle region. Once in the middle region, only Species 2 increases. That means the population of Species 1 is driven



**Figure 16.16.** Flow across the phase space, as explained in Chapter 10, converging on a stable equilibrium where Species 2 excludes Species 1. ( $r_1 = 0.75$ ,  $r_2 = 0.52$ ,  $s_{12} = -1.875$ ,  $s_{21} = -0.533$ ,  $s_{11} = s_{22} = -1$ ).

leftward, toward lower values of  $N_1$ , while the population of Species 2 is driven upward, toward higher values of  $N_2$ .

These dynamics show up in the flow diagram of Figure 16.16. The origin  $(0,0)$  is an unstable equilibrium. In this single-resource system, any populations near extinction, but not completely extinct, increase until they hit the middle region. The horizontal axis has another unstable equilibrium, where Species 1 is at its carrying capacity and Species 2 is extinct  $(-r_1/s_{1,1}, 0)$ . Any populations near that unstable equilibrium soon arrive in the middle region. All populations

not precisely on one of those two unstable equilibria converge on the red disc on the vertical axis, where Species 2 is at its carrying capacity,  $K_2 = -r_2/s_{2,2}$ , and Species 1 is extinct  $(0, -r_2/s_{2,2})$ . This equilibrium is called a “global attractor.”

**P**hase spaces thus provide another view of competitive exclusion, the theory of which applies at least to two species competing for a single resource at equilibrium.

## 16.6 Multiple resource phase space

As the next step, consider the case of two essential resources. This can be done mathematically following the approach we used earlier for a single resource.

Call the two resources  $R_A$  and  $R_B$ . Suppose that of the total of these two resources used by Species 1, a proportion  $p_1$  is Resource A and therefore a proportion  $q_1 = 1 - p_1$  is Resource B. Likewise, for Species 2 a proportion  $p_2$  is Resource A and  $q_2 = 1 - p_2$  is Resource B.

This is confusing, so for a clarifying example, suppose  $R_A$  is phosphate,  $\text{PO}_4$ , and  $R_B$  is silicate,  $\text{SiO}_2$ , both essential to two species of algae in a waterway. Take Species 1 to be an *Asterionella* species and Species 2 to be a *Cyclotella* species, as in a pioneering study by David Tilman (1977). In this case, Species 1 needs phosphate and silicate resources in about a 1:99 ratio, while Species 2 needs them in about a 6:94 ratio. If silicate is low, Species 1 will thus suffer first, since it needs a larger proportion of it, while Species 2 will suffer first if phosphate is low, for the related reason. Here it would be  $p_1 = 0.01$ ,  $q_1 = 1 - p_1 = 0.99$  for the use of Resources

A and B by Species 1, and  $p_2 = 0.06$ ,  $q_1 = 1 - p_1 = 0.94$  for use by Species 2.

With  $u_1$  being the total amount of resource tied up by each individual of Species 1,  $p_1 u_1$  will be the amount of Resource A tied up by Species 1 and  $q_1 u_1$  the amount of Resource B tied up the same way. Similarly,  $p_2 u_2$  will be the amount of Resource A tied up by each individual of Species 2 and  $q_2 u_2$  the amount of Resource B. Also, assume as before that the resources under consideration disappear from the environment when they are taken up by individuals newly born, are released immediately when individuals die.

With this in mind, the resources remaining at any time, as functions of the maximum resource and the abundance of each species, will be

$$\begin{aligned} R_A &= R_{A\max} - p_1 u_1 N_1 - p_2 u_2 N_2 \\ R_B &= R_{B\max} - q_1 u_1 N_1 - q_2 u_2 N_2 \end{aligned} \quad (16.9)$$

Suppose that populations of Species 1 and 2 grow based on which resource is closest to the  $R^*$  experienced by that species for the resource. This can be represented by the “min” function,  $\min(a, b)$ , which selects the smaller of two values. For example,  $\min(200, 10) = 10$ ,  $\min(-200, 10) = -200$ . Now the two-species, two-resource growth equations, generalizing the single-species, single-resource growth in Equation 16.1, are

$$\begin{aligned} \frac{1}{N_1} \frac{dN_1}{dt} &= m_1 \min(R_A - R_{1A}^*, R_B - R_{1B}^*) \\ \frac{1}{N_2} \frac{dN_2}{dt} &= m_2 \min(R_A - R_{2A}^*, R_B - R_{2B}^*). \end{aligned}$$



This could be refined, so that the growth rates  $m_1$  and  $m_2$  would depend on which resource was limiting, but this does not matter in the present analysis.

If the species are similar enough and the resource level is such that they are limited by the same resource, one will tend to be competitively excluded, as in the previous section. But if the two species are quite different, they can be limited by different resources and the equations can be simplified.

$$\begin{aligned}\frac{1}{N_1} \frac{dN_1}{dt} &= m_1(R_A - R_{1A}^*) \\ \frac{1}{N_2} \frac{dN_2}{dt} &= m_2(R_B - R_{2B}^*)\end{aligned}\tag{16.10}$$

Some algebra will reveal the basic properties. If you substitute the expressions for  $R_1$  and  $R_2$  from Equation 16.9 into Equation 16.10 you will get

$$\begin{aligned}\frac{1}{N_1} \frac{dN_1}{dt} &= m_1 (R_{A\max} - p_1 u_1 N_1 - p_2 u_2 N_2 - R_{1A}^*) \\ \frac{1}{N_2} \frac{dN_2}{dt} &= m_2 (R_{B\max} - q_1 u_1 N_1 - q_2 u_2 N_2 - R_{2B}^*)\end{aligned}$$

Now if you expand, collect, and rearrange terms, you get this equivalent form:

$$\begin{aligned}
 \frac{1}{N_1} \frac{dN_1}{dt} &= m_1 (R_{A_{\max}} - R_{A1}^*) - m_1 p_1 u_1 N_1 - m_1 p_2 u_2 N_2 \\
 \frac{1}{N_2} \frac{dN_2}{dt} &= m_2 (R_{B_{\max}} - R_{B2}^*) - m_2 q_2 u_2 N_2 - m_2 q_1 u_1 N_1
 \end{aligned}
 \tag{16.11}$$

$\begin{array}{ccc} \uparrow & \uparrow & \uparrow \\ r_i & s_{i,i} N_i & s_{i,j} N_j \end{array}$

Notice that, again, a mechanistic model with measurable parameters is just the general ecological RSN model in disguise.

The RSN formulation can expose the possibilities of two-resource situations in phase space. The isoclines are Equations 16.7 and 16.8 of this chapter, with slopes  $-s_{1,1}/s_{1,2}$  and  $-s_{2,1}/s_{2,2}$  for Species 1 and 2, respectively.

These two slopes can be written in terms of the resource. With the values for  $s_{i,j}$  from Equation 16.11 ( $s_{1,1} = -m_1 p_1 u_1$ ,  $s_{1,2} = -m_1 p_2 u_2$ ,  $s_{2,1} = -m_2 q_1 u_1$ , and  $s_{2,2} = -m_2 q_2 u_2$ ), the slopes of the isoclines become

$$\begin{aligned}
 \frac{s_{1,1}}{s_{1,2}} &= \frac{-m_1 p_1 u_1}{-m_1 p_2 u_2} = \frac{u_1}{u_2} \frac{p_1}{p_2} \\
 \frac{s_{2,1}}{s_{2,2}} &= \frac{-m_2 q_1 u_1}{-m_2 q_2 u_2} = \frac{u_1}{u_2} \frac{1 - p_1}{1 - p_2}
 \end{aligned}$$

First notice that if the two species use the two resources in equal proportions (if  $p_1 = p_2$ ), both slopes become  $u_1/u_2$ .

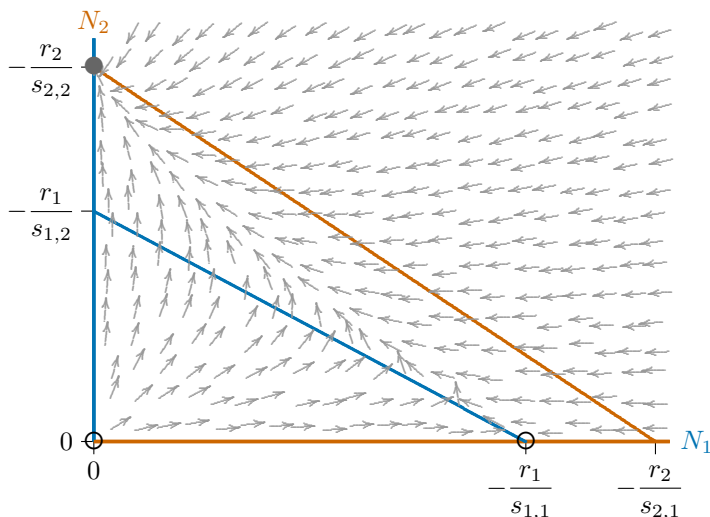
The slopes are parallel, as in the single-resource case in Figures 16.13 through 16.16. Therefore, if two species use two different resources identically—that is, in equal proportions—they do not coexist. Coexistence requires some difference in how they use resources.

**H**owever, using the resources differently does not guarantee coexistence. Depending on their  $p$ 's and  $q$ 's, one isocline could still enclose the other completely. Figure 16.17 has the same properties as Figure 16.16. Everywhere below the red isocline, Species 2 will increase, including the broad band between the red and blue isoclines where Species 1 will decrease.

If the blue and red isoclines are reversed, the result is similar, but with Species 1 excluding Species 2. Figure 16.18 shows this, with the arrows reversed as Species 1 increases everywhere below the blue isocline, including the broad band between the isoclines where Species 2 decreases.

In all three cases, from Figures 16.16 to 16.18, the system has three equilibria—at the origin  $(0, 0)$ , where both species are absent, at the carrying capacity  $K_1$  for Species 1 alone  $(-r_1/s_{1,1}, 0)$ , and at the carrying capacity  $K_2$  for Species 2 alone  $(0, -r_2/s_{2,2})$ . The origin is unstable and only one of the other two equilibria is stable, depending on which isocline encloses the other.

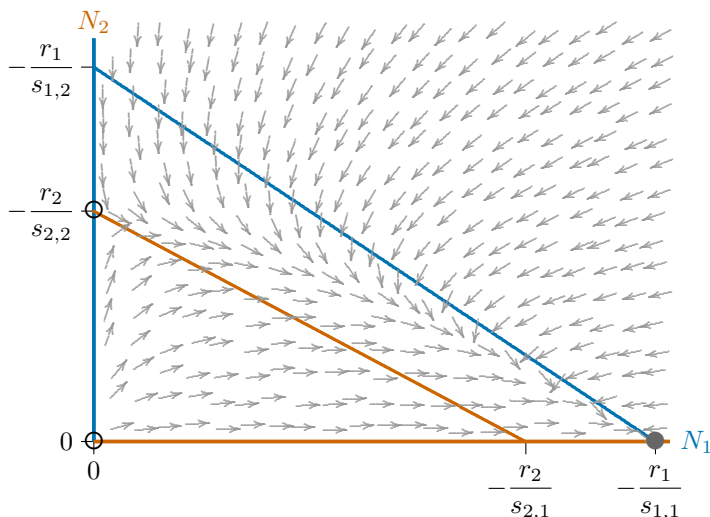
**F**igures 16.17 and 16.18 can be combined to give each species a chance to exclude the other, depending on circumstances. This means not allowing one isocline to completely enclose the other, as in Figure 16.19. Intersecting isoclines introduce



**Figure 16.17.** Two species using resources differently, with Species 2 excluding Species 1. ( $r_1 = 0.75$ ,  $r_2 = 0.65$ ,  $s_{12} = -1.875$ ,  $s_{21} = -0.666$ ,  $s_{11} = s_{22} = -1$ )

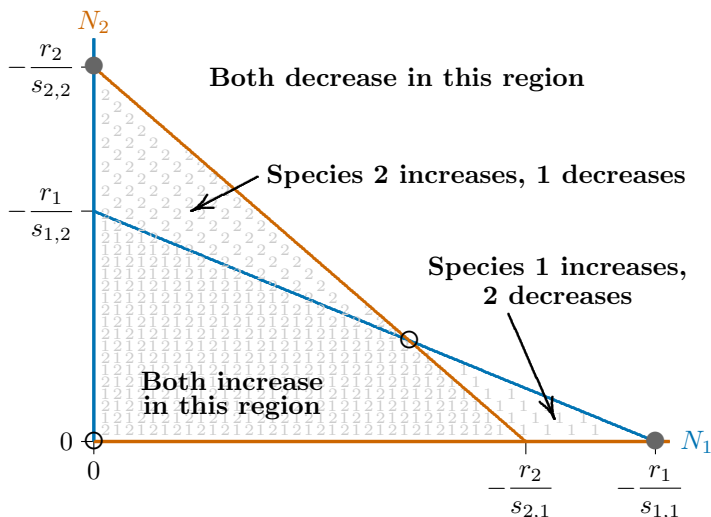
a fourth equilibrium at the interior of the phase space. This equilibrium is unstable, marked with an open circle, and the two equilibria for the individual species, on the axes, are stable. They are no longer “globally stable,” however, since only local regions of the phase space lead to either of them.

Depending on where the populations start, one of the two species will exclude the other. A curve called a “separatrix,”★ dividing these starting points according to which species will exclude the other, is shown with the dashed black line in Figure 16.20. That separatrix corresponds to a long curved ridge



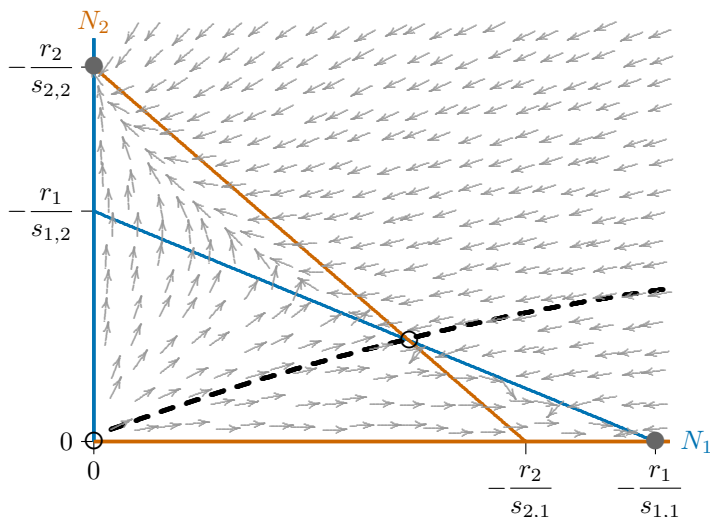
**Figure 16.18.** The opposite of Figure 16.17, with Species 1 excluding Species 2. ( $r_1 = 0.975$ ,  $r_2 = 0.4$ ,  $s_{12} = -1.5$ ,  $s_{21} = -0.533$ ,  $s_{11} = s_{22} = -1$ ).

in any surface above the phase space, as described in Chapter 10. It necessarily passes through the unstable interior equilibrium. Here it is a simple curve, though in some cases (such as the Mandelbrot system,★ not representing competition), related curves can be infinitely complex.



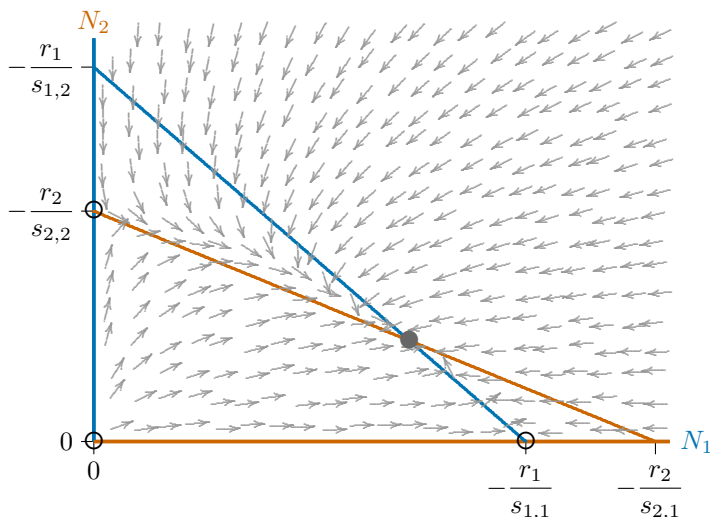
**Figure 16.19.** Isoclines intersecting in a way that allows each species to exclude the other, depending on starting conditions.

Finally, the isoclines can intersect in the opposite way, as in Figure 16.21. In this case, neither species has any region where its isocline encloses the other, as seen in each of the phase spaces of Figures 16.16 through 16.20. What will happen when neither species can exclude the other in any part of the phase space? They are forced to coexist. The individual equilibria on the axes become unstable and the interior equilibrium becomes stable—indeed, globally stable.



**Figure 16.20.** Flow in the bistable system of Figure 16.19. The black dashed line is a separatrix, dividing the phase space into regions that reach one stable equilibrium or the other. ( $r_1=0.975$ ,  $r_2=0.65$ ,  $s_{12}=-2.437$ ,  $s_{21}=-0.866$ ,  $s_{11}=s_{22}=-1$ ).

**I**n summary, the isoclines in competitive systems have four different configurations, as in Figure 16.22. Cases 1 and 2 can represent competition for a single resource or, equivalently, competition for two different resources that the two species handle identically. One of the two is a superior competitor that excludes the other. Case 3 is “bistable,” where either of the species can exclude the other, depending on how the system starts out. Finally, Case 4 is globally stable, where neither species can exclude the other, and stable coexistence



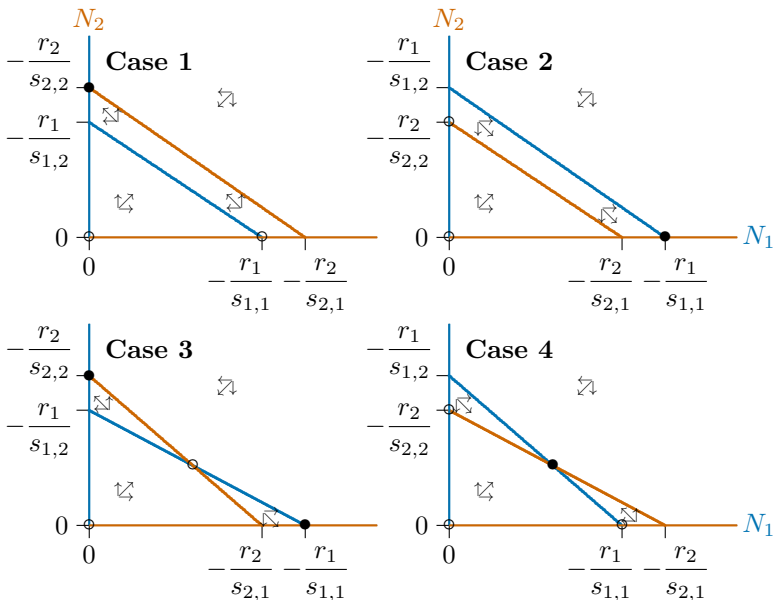
**Figure 16.21.** *Isoclines intersecting at a globally stable coexistence. ( $r_1 = 0.75$ ,  $r_2 = 0.4$ ,  $s_{12} = -1.153$ ,  $s_{21} = -0.410$ ,  $s_{11} = s_{22} = -1$ ).*

prevails. Cases 3 and 4 can represent competition for two different resources.

## 16.7 Lotka–Volterra formulation

Competition equations are usually presented in textbooks as the Lotka–Volterra competition model.★ This first appeared in the ecological literature in the 1920s and is defined not





**Figure 16.22.** Case 1: Species 2 excludes Species 1. Case 2: Species 1 excludes Species 2. Case 3: one excludes the other, depending on starting conditions. Case 4: both species coexist.

just in terms of the interactions among species, but also in terms of the species' carrying capacities, as follows.

$$\begin{aligned} \frac{1}{N_1} \frac{dN_1}{dt} &= r_1 \left( 1 - \frac{N_1 + a_{1,2}N_2}{K_1} \right) \\ \frac{1}{N_2} \frac{dN_2}{dt} &= r_2 \left( 1 - \frac{N_2 + a_{2,1}N_1}{K_2} \right) \end{aligned} \quad (16.12)$$

$K_1$  and  $K_2$  are the carrying capacities for Species 1 and 2, respectively. Parameters  $a_{1,2}$  and  $a_{2,1}$  represent the interference by each species on the other. If  $a_{1,2} = 2$ , for example, each individual of Species 2 interferes with the growth of Species 1 as if it were two individuals of Species 1. If, on the other hand,  $a_{1,2} = 1/2$ , it takes two individuals of Species 2 to have the same negative effect on the growth of Species 1 as one individual of Species 1 itself.

To compare this with the RSN formulation, represent Equation 16.12 with  $i$  and  $j$  subscripts

$$\frac{1}{N_i} \frac{dN_i}{dt} = r_i \left( 1 - \frac{N_i + a_{i,j}N_j}{K_i} \right)$$

and multiply the right hand side through by  $r_i$ ,

$$\frac{1}{N_i} \frac{dN_i}{dt} = r_i - \frac{r_i}{K_i} N_i - \frac{a_{i,j}r_i}{K_i} N_j$$

This shows that the Lotka–Volterra formulation is isomorphic to the RSN formulation. All conclusions about competitive systems examined thus far apply to the Lotka–Volterra formulation as well, with the appropriate translation of parameters. Parameter  $r_i$  is the same in both in the Lotka–Volterra formulation and the RSN formulation, but  $s_{i,i} = -r_i/K_i$  and  $s_{i,j} = -a_{i,j} r_i/K_i$ .

**B**eware, however, of a widely quoted statement derived from this formulation that appears throughout the ecological literature and textbooks. Statements like “Coexistence requires that each species inhibit itself more than it inhibits the other

**Box 16.1.**

*Coexistence in the Lotka–Volterra model requires that each species be able to increase from low densities when the other species is at its single-species equilibrium.*

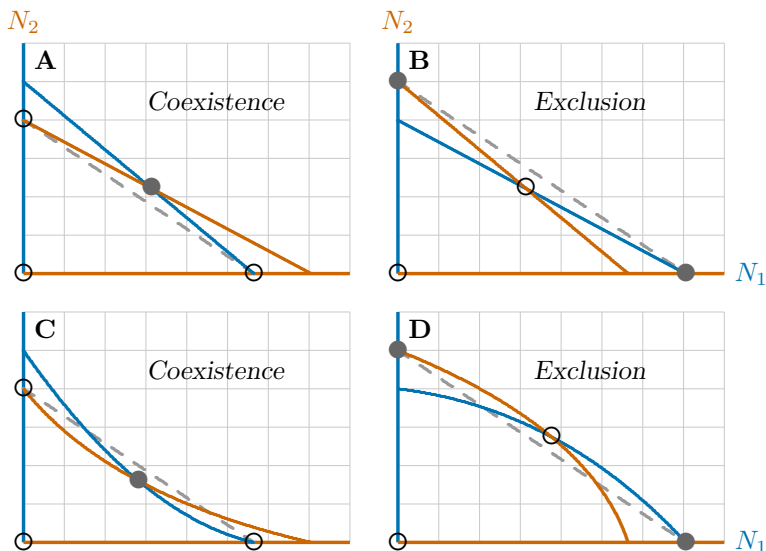
species” are abundant in textbooks and in the ecological literature. Alas, those statements are not correct.

To see this, examine Figure 16.21. Here Species 1 inhibits itself with  $s_{11} = -1$ , while it inhibits the other species more strongly with  $s_{12} = -1.153$ . Yet there is global coexistence. Evidently, coexistence *does not* require that each species inhibit itself more than it inhibits the other, as in the conventional wisdom.

The confusion in the literature has apparently emerged from the presence of the carrying capacity terms,  $K_1$  and  $K_2$ , in the Lotka–Volterra formulation. These terms obscure the effects of the interaction terms,  $a_{1,2}$  and  $a_{2,1}$ , when carrying capacities differ between the species.

What, then, is a correct statement about coexistence? It can be put in terms of increasing from low densities, as shown in Box 16.1. The qualifying phrase “*from low densities*” is required, because the species not present can increase from high densities in a bistable system, as in Figure 16.20, and flip it to the other state, even though coexistence cannot occur.

Another way in which coexistence has been explained is by Vandermeer (1981 *Bioscience*), connecting coexistence with a certain kind of “overyielding,” wherein two crops require



**Figure 16.23.** Coexistence in terms of a kind of overyielding (Vandermeer 1981, Bioscience).

less land for the same annual productivity when growing together than when growing apart. The test is whether the joint equilibrium is above a line connecting the single-species equilibria (dashed gray in Figure 16.23 A) or below the line (Figure 16.23 B).

This view is correct for models we have been considering with straight-line isoclines, but incorrect for more general models with curved isoclines (Figure 16.23 C, D). The statement in Box 16.1, however, holds true in each of these cases.

All things considered, rather than relying on rules of thumb, it can be better to evaluate a system directly, for example with the methods of eigenvectors and eigenvalues described in Chapter 10.



## Chapter 17

### Mutualism

In Equation 8.1, mutualism occurs when the interaction terms,  $s_{1,2}$  and  $s_{2,1}$ , are both positive. This is the defining feature of mutualism. The self-engagement terms,  $s_{1,1}$  and  $s_{2,2}$ , may be positive or negative, and the intrinsic growth terms,  $r_1$  and  $r_2$ , may also be positive or negative.

If both growth terms  $r_i$  are positive, then either species can survive on its own, without the presence of the other. This is called “facultative mutualism.” An example is the mutualism between oxpecker and warthog (Figure 9.2 left). Oxpeckers have other sources for food, and warthogs may suffer but likely not die from larger parasite loads.

If the  $r_i$  are both negative, then neither species can survive on its own without the presence of the other. This is called “obligate mutualism.” An example is lichen, composed of an algae and a fungus. If the fungus alone is placed on a rock, it will die. Although it can eat rock—or, more accurately, can dissolve nutrients from rock—it cannot produce carbon compounds from rock. And if the algae alone is placed on a rock, it will die. Although it can produce carbon compounds from the air through photosynthesis, it cannot eat rock. But



**Figure 17.1.** *Photosynthesis is the basis of many mutualisms. Euglena is a protist–chloroplast combination that can fix carbon dioxide from the water, changing the nature of the protist, and can move distances following nutrients, supporting the chloroplast. Chloroplasts appear to be much-modified cyanobacteria, rendered wholly dependent on their partners by eons of evolution (left, through a microscope). Lichens are fungal–algal combinations in which the algal component can fix carbon and the fungal component can dissolve nutrients from rock (middle, shoulder height). Coral are anthozoa—marine animals with stinging tentacles to capture food—that are often reef-building and associated with marine algae. A significant fraction of the world’s carbon is sequestered in coral reefs (right, from space).*

the two together become a perfect partnership, each covering the other’s weaknesses.

When  $r_1$  is positive and  $r_2$  is negative, or vice versa, it is a partially obligate mutualism. One species depends on a second, but the second can get along without the first. This is a mathematical possibility, and some cases such as chloroplast–euglena may be examples (Figure 17.1 left), where the chloroplast cannot live without the protist, but the protist can.

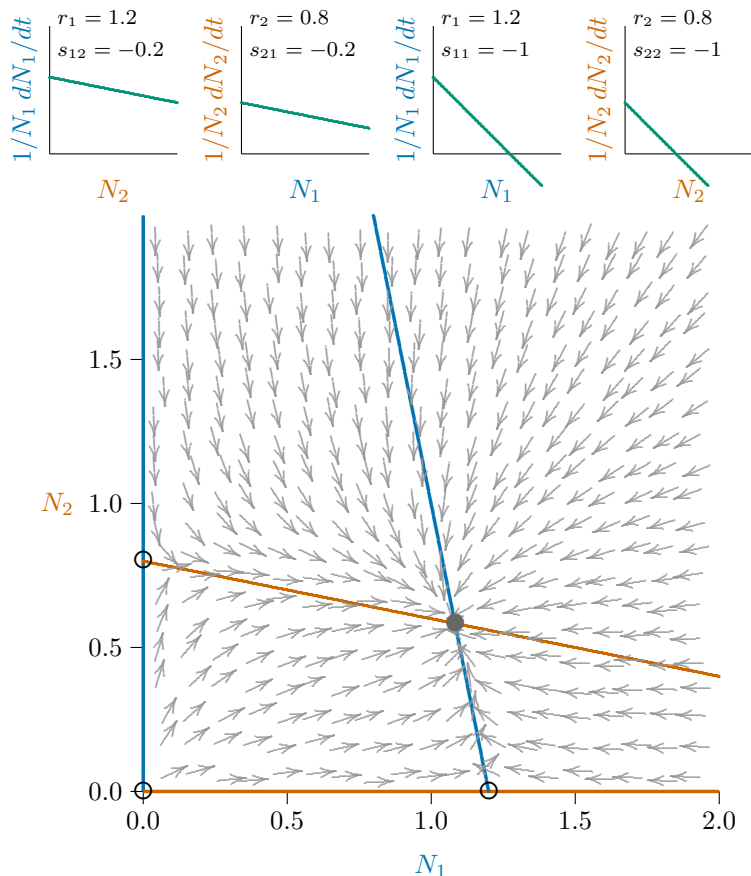
Besides obligate versus facultative mutualism, there is another major distinction. This is between “restrained” and



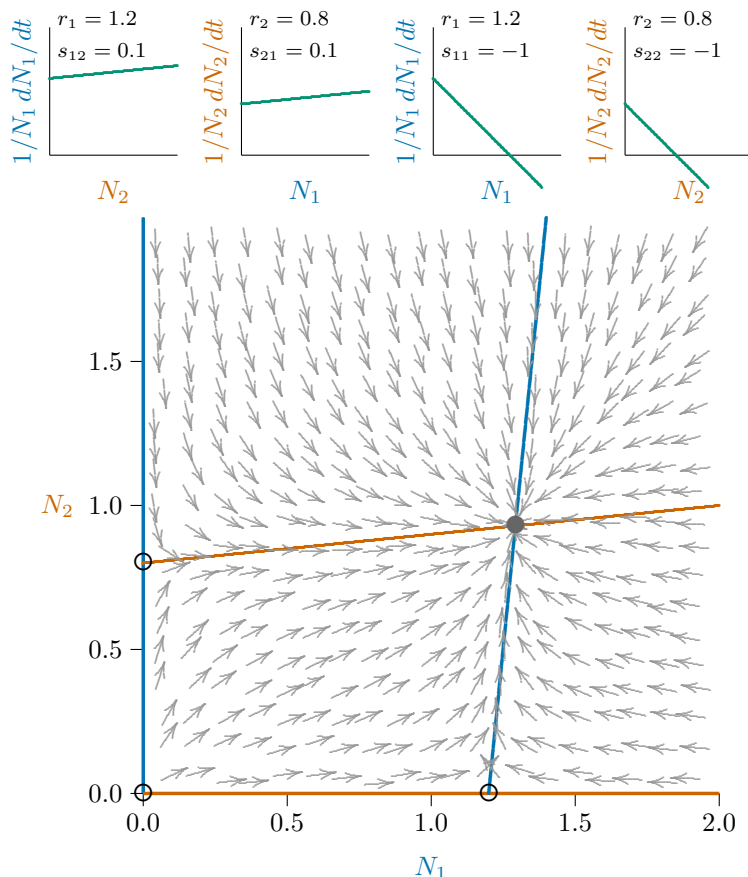
“unrestrained” mutualism. This distinction is not typically made in textbooks because it is related to the difference between logistic and orthologistic population growth, which typically is not covered.

When self-limiting effects of terms  $s_{1,1}$  and  $s_{2,2}$  are stronger than the inter-species enhancement terms  $s_{1,2}$  and  $s_{2,1}$ , the mutualistic pair has a carrying capacity that can be computed from the properties of the individual species. They reach their joint carrying capacity along a path that looks like logistic growth, and is identical in form to that of two competing species that coexist and reach a joint carrying capacity. However, when the self-limiting effects of  $s_{1,1}$  and  $s_{2,2}$  are weaker than the inter-species enhancement terms  $s_{1,2}$  and  $s_{2,1}$ , the carrying capacity of the pair of species cannot be computed from the value of those parameters, and they increase ever more rapidly until some other limitation is hit.

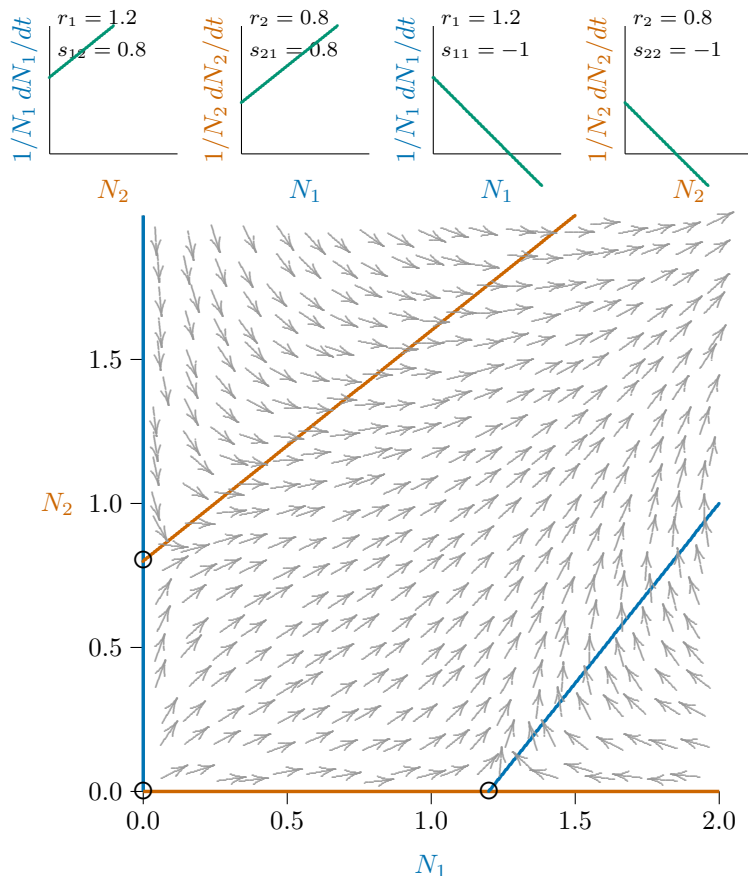
Think about lichen again. The carrying capacity of each species is essentially zero when they are living separately on the surface of a rock. Together, however, they can cover the rock, and their joint carrying capacity on Earth is related to the total area of rocks on Earth—plus other suitable habitat such as the bark of trees, the exterior surface of an automobile junked and neglected for decades, and myriad other surfaces otherwise uninhabitable. The area of rocks in the world, and other suitable surfaces, certainly is not part of the  $r_i$  and  $s_{i,j}$  parameters! This is quite unlike the situation for competition and predation, in which the joint carrying capacity is encoded in the parameters. Why this should be is revealed by some diagrams and corresponding mathematics.



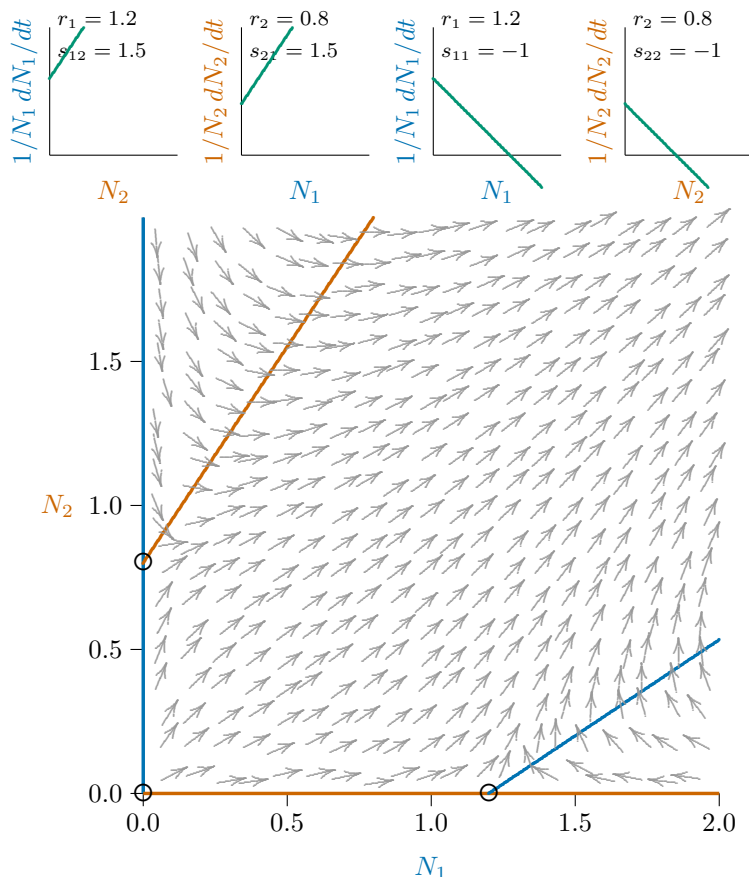
**Figure 17.2.** Phase space for competition weaker than that of Figure 10.11. The joint equilibrium (black-filled circle) is closer along the axes to the individual carrying capacities (open circles).



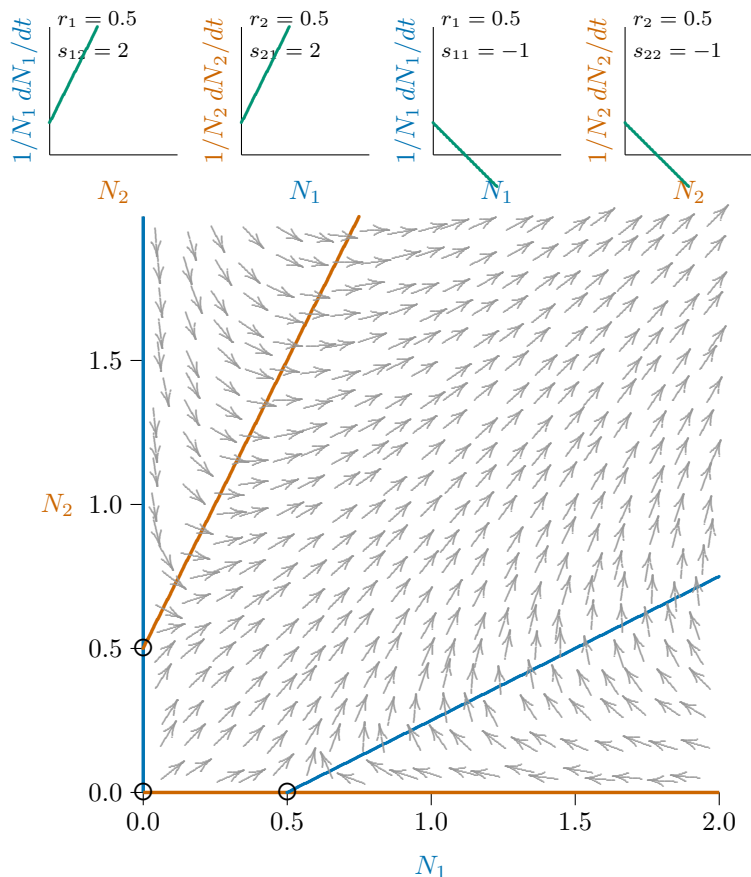
**Figure 17.3.** Phase space for mild mutualism, causing the opposite effect of that shown in Figure 17.2. The joint equilibrium is larger than the individual carrying capacities.



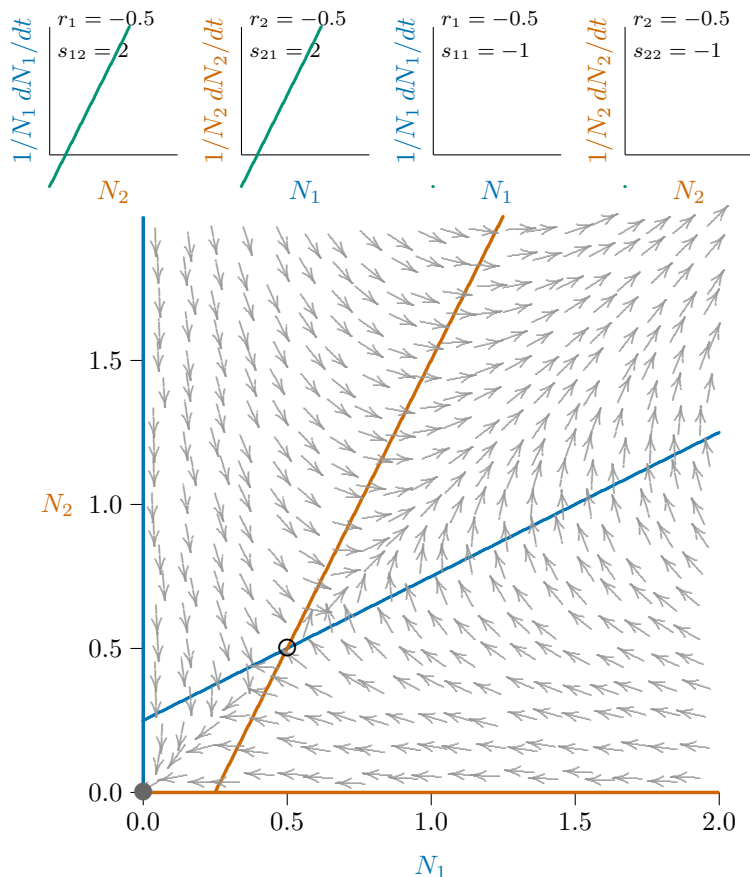
**Figure 17.4.** Phase space for stronger mutualism, but still restrained, because a joint equilibrium still exists (though far off the chart at the intersection of the red and blue isoclines).



**Figure 17.5.** With slightly stronger mutualism still, the joint equilibrium vanishes—cannot be determined from the parameters—and the mutualistic relationship becomes “unrestrained.”



**Figure 17.6.** As mutualistic species become more dependent upon each other, their individual carrying capacities become smaller (open circles here are closer to the origin).



**Figure 17.7.** Finally, in obligate mutualisms, individual carrying capacities vanish and an Allee point arises (open circle). Extinction becomes a present danger (closed circle).

## 17.1 Phase diagrams

The principles can be visualized in phase diagrams, with arrows showing how populations change. Earlier, Figure 10.11 showed strong competition with coexistence at equilibrium, as could be the case if the species were competing for two different resources. Nonetheless, each species restricts the other to much lower levels than it could maintain on its own. Weaker competition means that each species is restricted less so each can maintain higher levels, as in Figure 17.2. You can tell this is competition because the two parameters  $s_{1,2}$  and  $s_{2,1}$  are both negative. This is shown in the negative slopes of the two diagrams in the upper left. The carrying capacity of each species together is only slightly reduced from the individual carrying capacities, which would be about 1.2 for Species 1 living alone and about 0.8 for Species 2 living alone. (for example, an average of 1.2 individuals per square meter, or 1,200,000 individuals per square mile if measured in millions). However, for species living together, the carrying capacity of each is slightly reduced, perhaps 10 to 20 percent.

In this case, by the way, the two species together have a higher total population than would be the case if either was living alone. This is called “over yielding,” and is a recurrent theme in studies of plant communities.

Figure 17.3 shows a similar situation, but now with the inter-species interaction terms  $s_{1,2}$  and  $s_{2,1}$  both positive, shown by the positive slopes in the two upper-left diagrams of the figure. It looks quite similar to Figure 17.2, but the two



together are each more abundant than they would be apart—the joint equilibrium is larger than the individual carrying capacities.

This joint equilibrium can be computed from the  $r_i$  and  $s_{i,j}$  parameters. It will occur where the growth of each species simultaneously reaches 0. You can find the numerical value for this equilibrium with pencil and paper by setting the first species growth rate to 0, solving for the populations of Species 1, substituting that into the equation for Species 2, and solving for when the growth of that species reaches 0. Alternatively, you can pose the problem to a symbolic mathematics program and ask it to solve the two equations simultaneously. In any case, you would start with both growth rates set to zero at equilibrium,

$$\frac{1}{N_1} \frac{dN_1}{dt} = r_1 + s_{1,1} N_1 + s_{1,2} N_2 = 1.2 - 1 N_1 + 0.1 N_2 = 0$$

$$\frac{1}{N_2} \frac{dN_2}{dt} = r_2 + s_{2,2} N_2 + s_{2,1} N_1 = 0.8 - 1 N_2 + 0.1 N_1 = 0$$

and end up with  $N_1 = 1.2929$  and  $N_2 = 0.929$ .

As mutualisms become stronger—meaning that the inter-specific interactions become more positive—the equilibrium point moves further out. It can be very large, as in in Figure 17.4, but, in restrained mutualism, the equilibrium is finite and computable from the parameters of the individual species.

On the other hand, when the inter-species enhancement terms are stronger still, a bifurcation occurs and the joint

equilibrium ceases to exist at all. (Figure 17.5). The calculated equilibrium point has, in effect, moved to infinity, or in a sense beyond, meaning that the carrying capacity cannot be computed from the parameters of the species and their interactions. Some further information is needed about the system.

Beyond this, the mutualists can become more dependent on each other, so that the  $r_i$  terms become smaller, as in Figure 17.6, or negative, as in Figure 17.7. The mutualism can be unrestrained even if the intrinsic growth rates  $r_i$  are negative. What arises is a kind of Allee point, where the populations run away if they start above that point, but decline to extinction if they start below.

## 17.2 Quasi-species

A new phenomenon arises in equations for unrestrained mutualism, one not possible for competition or predation. It can be shown that unrestrained mutualists are pulled into fixed ratios which are based on how their interaction terms differ from their self-limiting terms. As populations grow and move toward these fixed ratios, the two equations governing the individual species collapse, in effect, into an equation of a single-species. This single species grows orthologistically, a form of growth you saw earlier in Figure 4.3. The system behaves mathematically as if only one species were participating.

What does the mathematical collapse to a single equation mean biologically? It suggests that the biological world

could respond analogously—that two actual species growing as unrestrained mutualists could intermingle into a single quasi-species—at least into the best approximation of a single species that biology could accomplish using genetically different entities. Lichen and the eukaryotic cell are examples, genetically separate but biologically merged. Indeed, lichens were thought to be individual species until the nineteenth century, and the eukaryotic cell was only accepted as the result of mutualistic combinations late in the twentieth.

It therefore appears that natural selection has not overlooked this possibility. In a community model with mutualistic species locked in approach to a singularity, the two mutualists may be replaced in the model by a new quasi-species, representing the two species jointly but ultimately having a non-singular form of population growth. The resulting quasi-species may grow without obvious inhibition toward a singularity, then switch to a different model, as you have seen for single-species models in Figure 4.4 and for our own species in Figure 6.3.

### 17.3 Our own species

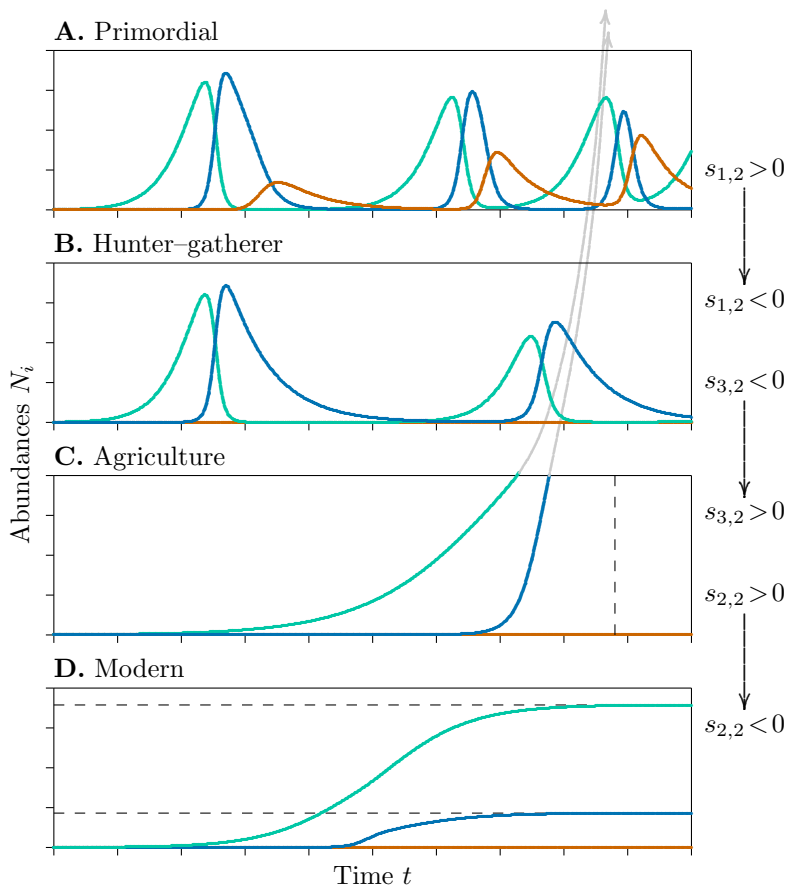
We reached our present numbers through a complex of mutualisms. A variety of increasingly refined crops and increasing domesticated animals acted as mutualists, switching our population dynamics from boom-and-bust predator-prey cycling (Figure 17.9A) to prolonged runaway growth (17.9B). Through cultivation of plants and animals that were formerly



**Figure 17.8.** *One of the most conspicuous mutualisms on the planet involves our species. Our mutualisms are biological, but have become technological as well, with teams of satellite-guided tractors navigating our fields with the power of a thousand horses.*

prey, agriculture increased the carrying capacity of the cultivated species, which in turn increased human carrying capacity, forming a positive feedback loop. It may seem dubious to consider domesticated plants and animals as our mutualists, but their parameters meet the mathematical requirements of mutualism. And both populations can expand so rapidly that they would soon exceed all former bounds.

Mutualisms in nature typically do not long follow the unrestrained growth toward astronomical levels shown in Figure 17.9B. Instead, natural mutualisms increase only until they are checked by some other force, such as predators or disease. Our ancestors, however, kept their mutualisms pure by eliminating third-species interferences. They hunted and killed predators of domesticated animals, weeded crops to eliminate plant competitors, and fenced crops to exclude herbivores. Indeed, the human species does not now dominate the earth, as often suggested. The mutualisms dominate. The joint biomass of cows, horses, pigs, chickens, and dogs



**Figure 17.9. Stages in human population dynamics.** Representative predator abundance is shown in red, prey abundance in green, and abundance and our ancestors in blue.

exceeds the biomass of humans, to say nothing of the biomass of crops. We did not get here alone.

We have recently outgrown the need for animal mutualists to power plows and support locomotion, substituting engines consuming fossil fuels instead. These are like synthetic mutualists. We also outgrew the need for animals to fertilize crops, substituting artificial nitrogen fertilizer created in Haber–Bosch process furnaces from the vast supply of nitrogen in the air. The need for animals and plants for clothing diminished with synthetic cloth and furs. All of these brought us to a partially non-biological world, still developing, where not even the carrying capacities of our living mutualists need be limiting.

However, advancing medicine and public health eventually decreased child mortality. Death rates fell and, later, birth rates began to fall even faster. The mutualisms remain, but—unexpectedly and abruptly—twelve millennia of rapidly accelerating population growth ended (Figures 6.3, 17.9C).

**A**s a closing note, in the twenty-first century, after only about fifty years of decelerating growth, the global population continues to increase. But, births in many societies have dropped below replacement levels in a final stage characterized by declines in the resident populations, compensated in many countries by immigration. The relative rapidity of this change may spill over into social disjunction between conditions of the present and memories of times past. It may also

foretell a future time when our species may voluntarily reduce populations to sustainable values yet unknown (dotted lines in Figure 17.9C).



**Figure 17.10.** *A complex of mutualisms are represented here. What are they? Dog and human together are one pairwise mutualism, among the oldest for our species. Sheep and humans are another. What else? Grass with sheep keeping the forest from invading? Humans protecting forests for firewood? Anything else?*

## Chapter 18

### Higher-order models

The RSN formulation of Equations 4.1 and 8.1 incorporate the classical competition, predation, and logistic equations of ecology, plus mutualistic and orthologistic equations that are not part of the classical set. For this, the parameters can remain constant.

But they are not constant in all cases. Volterra<sup>★</sup> (1928) considered parameters that vary through time, but more generally the parameters can be functions of population density as well. In this way the RSN formulation can be extended to cover not just the classical equations of ecology and related equations, but any equations of ecology whatever, as with Equation 4.3, proposed by Kolomogorov.<sup>★</sup>

#### 18.1 One-species examples

To see the basic idea, start with a single species. With variable parameters, population growth for a single species (Equation 4.1) can be written as follows, with the growth rate  $r$  and the density dependence term  $s$  depending on the population level  $N$  and optionally on the time  $t$ .

$$\frac{1}{N} \frac{dN}{dt} = r(N, t) + s(N, t) N \quad (18.1)$$



Because anything can be embedded in the term  $r(N, t)$ , or in the corresponding  $s(N, t)$ , the equation is perfectly general and can cover any ecological situation for a single species modelled by a differential equation. A basic example, which you have already seen for human population growth, is where the parameters are approximately constant for long periods, but change at certain “bifurcation” events. The parameters for human population growth changed abruptly at the beginning of the modern era, resulting in overall population dynamics that were neither orthologistic nor logistic, but a piecewise combination of the two. In that case the two were blended by varying the parameters as follows.

$$\frac{1}{N} \frac{dN}{dt} = \begin{cases} -0.001185 + 0.00684 N, & \text{when } N \leq 3.28 \text{ billion} \\ 0.03077 - 0.00289 N, & \text{when } N > 3.28 \text{ billion} \end{cases}$$

This led to the population growth curve of Figure 6.3, which nicely modeled human population growth over the centuries.

Human population growth called for a piecewise blending of the parameters, because the parameters changed rather abruptly from one constant set to another. The parameters can also be blended continuously for parameters that change gradually.

For example, take an orthologistic equation,  $1/N \, dN/dt = -2 + 2N$ , and a logistic equation,  $1/N \, dN/dt = 4 - 2N$ , and consider  $N$  as it ranges from 0 to 1. Have the orthologistic equation apply exactly as  $N$  approaches 0, and the logistic equation apply exactly when  $N$  reaches 1. Then let  $r$  change

uniformly from  $-2$  to  $+4$  and  $s$  change uniformly from  $+2$  to  $-2$  as  $N$  goes from 0 to 1, as follows.

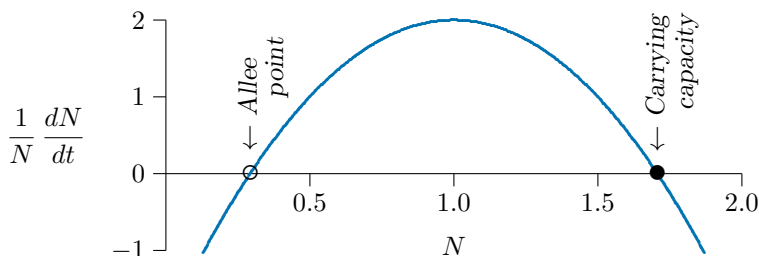
$$r(N, t) = 6N - 2$$

$$s(N, t) = -4N + 2$$

Plugging that into Equation 18.1 gives

$$\begin{aligned} \frac{1}{N} \frac{dN}{dt} &= (6N - 2) + (-4N + 2) N \\ &= -2 + 8N - 4N^2 \\ &= r + sN + s_2 N^2 \end{aligned}$$

This kind of blending between orthologistic and logistic has simply added one more term to the population growth equation, an  $N^2$  term—one of the terms proposed by Hutchinson★ (Equation 4.2). The result is graphed in Figure 18.1.



**Figure 18.1.** Orthologistic and logistic equations smoothly blended.

This smoothly blends the orthologistic, which has an Allee point but no carrying capacity, with the logistic, which has a carrying capacity with no Allee point, providing both in the blended curve of Figure 18.1. The curve has an Allee point at about  $N=0.3$  and a carrying capacity at about  $N=1.7$ . Compare this with the piecewise blending depicted earlier in Figure 4.4.

## 18.2 Two-species blending

Blending two-species systems is a similar process, but has more options in the parameters. Equation 18.2 is an example with limited options that produced the phase spaces in Figures 10.3 through 10.5.

$$\begin{aligned}\frac{1}{N_1} \frac{dN_1}{dt} &= r_1(N_1) + s_{1,1} N_1 + s_{1,2}(N_1) N_2 \\ \frac{1}{N_2} \frac{dN_2}{dt} &= r_2(N_2) + s_{2,2} N_2 + s_{2,1}(N_2) N_1\end{aligned}\tag{18.2}$$

Changing the parameters uniformly from a  $b$  value when the corresponding  $N$  value is 0 to an  $a + b$  value when the corresponding  $N$  value is 1 is analogous to the blending that produced Figure 4.4. The parameters would vary as follows, using four distinct  $a$  values ( $a_1, a_2, a_{1,2}, a_{2,1}$ ), plus four distinct  $b$  values with matching subscripts ( $b_1, b_2, b_{1,2}, b_{2,1}$ ).

$$\begin{aligned}r_1(N_1) &= a_1 N_1 + b_1, & s_{1,2}(N_1) &= a_{1,2} N_1 + b_{1,2} \\ r_2(N_2) &= a_2 N_2 + b_2, & s_{2,1}(N_2) &= a_{2,1} N_2 + b_{2,1}\end{aligned}$$

Substituting the above into Equation 18.2 and collecting terms gives an equation having all the RSN terms present, but now with a cross-product in terms of  $N_1N_2$  added at the end:

$$\begin{aligned}\frac{1}{N_1} \frac{dN_1}{dt} &= b_1 + (a_1 + s_{1,1})N_1 + b_{1,2}N_2 + a_{1,2}N_1N_2 \\ \frac{1}{N_2} \frac{dN_2}{dt} &= b_2 + (a_2 + s_{2,2})N_2 + b_{2,1}N_1 + a_{2,1}N_1N_2\end{aligned}\tag{18.3}$$

In the specific case of Figures 10.3 through 10.5, we used  $s_{1,1} = s_{2,2} = -0.98$  and

$$\begin{aligned}r_1(N_1) &= 0.75N_1 - 0.5 & s_{1,2}(N_1) &= -1.15N_1 + 2.5 \\ r_2(N_2) &= 0.75N_2 - 0.5 & s_{2,1}(N_2) &= -0.45N_2 + 1.3\end{aligned}$$

which gave

$$\begin{aligned}\frac{1}{N_1} \frac{dN_1}{dt} &= -0.5 - 0.23N_1 + 2.50N_2 - 1.15 N_1N_2 \\ \frac{1}{N_2} \frac{dN_2}{dt} &= -0.5 - 0.98N_2 + 2.05N_1 - 0.45 N_1N_2\end{aligned}$$

for the flow in the figures.

## 18.3 A way of organizing

The methods we have described in this chapter provide an organized way of designing higher-order models of ecological interactions. Characteristics of the individual models purely in RSN form can be mixed and matched as needed to produce the higher-order model, then the resulting parameters can be fit to observations or modelling needs.



For example, the bistable phase space in Figures 10.3 through 10.5, with an unstable Allee point combined with a stable carrying capacity, was easy to achieve by combining sub-models, each with one of those characteristics. The result was simply an RSN system with an  $N_1N_2$  cross-product term added, but how easy would it have been to conceive that term *a priori* and perceive its sufficiency?

Moreover, a blended model in the form of Equation 18.2 can be visualized in terms of (1) the intrinsic growth rate of each species, (2) how each species affects the other, (3) how each species affects itself, and (4) how those effects change with population densities. In a way, any higher-order system constructed in this way can be viewed as an RSN system at every point, yet as a higher-order system overall.

**I**n summary, we cautiously recommend this method of creating and organizing ecological models, and are eager to hear of successes and failures you might have with it.

The characters acting in this book—the equations of population growth, the parameters and their relationships, the graphs and phase planes—live in variations and disguises within an enormous variety of actual ecological applications, detailed in thousands of scientific papers you will be able to sample as your journey continues. We hope you have enjoyed this introductory book and that it has been useful. We welcome your comments on any aspects at all. An ebook is never finished but can constantly be improved.

—C.L., S.L., A.C.

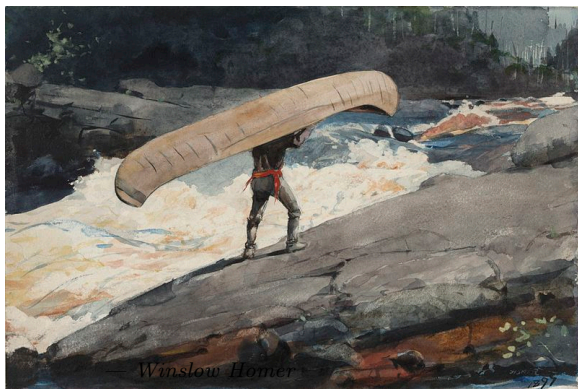


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